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ERRATA

Page 65, line 13
for Sholz read Scholz

Page 105, line 19
for cornoso read carnoso

Page 106
add Drawn by Leslie A. Garay

Page 151, line 8
for basem read basim

Page 123, line 6
for lanceoloto read lanceolato

Page 172
reverse upper and lower legends

Page 278
after *Banisteriopsis inebrians* add *Banisteriopsis quitensis* (Ndz.)
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Page 283, line 7
for *utilissima* read *esculenta*

Page 310, line 1
for florium read florum

Page 316, line 9
for *Hostmanii* read *Hostmannii*

Page 317, line 18
for *specimine* read *speciminis*

Page 317, line 26
for essensial read essential

Page 323, line 22
for Gary read Garay

Page 324, line 1
for (*Lehm.*) read (*Lem.*)

Page 325, line 8
for Barb. Rod. read Barb.-Rodr.

Page 375, line 14
for terminal read subterminal

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THE IDENTITY OF THE MALPIGHIACEOUS NARCOTICS OF SOUTH AMERICA

BY

RICHARD EVANS SCHULTES

> This is all I have seen and learnt of caapi or aya-huasca. . . . Some traveller who may follow my steps with greater resources at his command, will, it is hoped, be able to bring away materials adequate for the complete analysis of this curious plant.
>
> *Richard Spruce*

I

THE New World narcotics to which man has attributed the most extraordinarily bizarre powers of altering the state of his body and mind hid out successfully from prying European eyes and were not discovered and identified botanically until about one hundred years ago. They remain, even to-day, the most poorly understood of the hallucinogens of the Americas and the narcotics whose identification is most baffling. Indeed, we may truthfully say that we stand merely on the threshold of our investigations into the botany, ethnology, history, pharmacology, chemistry and therapeutics of that complex of intoxicants known as *ayahuasca*, *caapi* or *yajé*.

II

The purpose of this paper is to summarize what is known about the identity of the malpighiaceous narcot-

ies and to try to make some order from the rather chaotic state which at present obtains. A survey of the literature has been made, and the information from this source is evaluated in the light of field experience in the northwestern part of the Amazon Valley which seems to be the centre of use of these narcotics. It is noteworthy that such a standard work as Hartwich (29) fails even to mention any intoxicant from the *Malpighiaceae*.

This present study, however, leaves much to be desired. Since references to the malpighiaceous narcotics are widely scattered throughout botanical, anthropological, geographical and travel literature, I can make no claim to completeness of coverage. By far the greatest number of the references in regard to the sources of these narcotics are of limited or doubtful value; nevertheless it has been thought best to cite all that have come to light. I might say categorically, however, that much careful and sustained field work must be done before anything approaching a full understanding of the problem may be attained.

Since this paper is concerned only with the identification of source-species, all discussion of the uses, effects, chemical constitution and ethnological importance of the narcotics themselves has been omitted.

The line drawings were made possible by a grant from the American Academy of Arts and Sciences, and publication of the illustrations has been done through a grant from the National Science Foundation. I express my appreciation to Miss Ruth Barton and Mr. Elmer W. Smith for the drawings reproduced herein.

III

When, in 1851, the botanical explorer Richard Spruce penetrated the upper Rio Negro basin in Amazonian Brazil, a new and fertile epoch opened for natural science

Plate I

1 Guahibo
2 Zaparo
3 Angatero
4 Mazan
5 Correguahe
6 Jivaro
7 Colorado
8 Cayapa
9 Ingano
10 Siona
11 Kofan
12 Tlolo
13 Bora
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15 Kubeo
16 Tukano
17 Maku
18 Desano
19 Gwanano
20 Yekwano
21 Makuna
22 Barasana
23 Tanimuka
24 Miraña
25 Yukuna
26 Taiwano
27 Kabuyari
28 Andoke
29 Bare
30 Baniva
31 Tariana
32 Tiyuka
33 Pioje
x unidentified tribes
STATUTE MILES
TRIBES REPORTED TO USE MALPIGHIACEOUS NARCOTICS (CAAPI, AYAHUASCA, YAJE)
Venezuela
Orinoco
Colombia
Ecuador
Peru
Brazil
Amazonas
Bolivia

in the New World. Undoubtedly, one of Spruce's greatest contributions to science was his discovery and ethnobotanical study of the curious *caapi*. He found the Tukanoan Indians of the Rio Uaupés and its affluents using *caapi* to induce for prophetic and divinatory purposes a narcosis characterized, amongst other strange effects, by frighteningly realistic colored visual hallucinations and a feeling of extreme and reckless bravery. This contribution included a precise identification, through flowering material, of a source of the narcotic, an hitherto undescribed species of a malpighiaceous liana. The liana, originally named *Banisteria Caapi* Spruce ex Griseb., is now correctly called *Banisteriopsis Caapi* (Spruce ex Griseb.) Morton. Although Spruce's observations were written down in his wonted preciseness in 1852, they were not published until the posthumous account of his travels appeared in 1908 (90). In 1852, finding *caapi* cultivated in quantity on the Rio Uaupés, he noted: "There were about a dozen well-grown plants of *caapi*, twining up to the tree-tops along the margin of the *roça* [a cultivated plot] and several smaller ones. It was fortunately in flower and young fruit, and I saw, not without surprise, that it belonged to the order Malpighiaceae and the genus *Banisteria*, of which I made it out to be an undescribed species and therefore called it *B. Caapi.*" (90)

Two years later, Spruce found *caapi* in use amongst the Guahibo Indians of the upper Orinoco in Colombia and Venezuela. Here the natives "not only drink an infusion, like those of the Uaupés, but also chew the dried stem, as some people do tobacco." Again, in 1857, whilst working in the Peruvian Andes, he encountered the Záparo Indians using a narcotic known as *ayahuasca*. He stated that he "again saw *caapi* planted" in the northeastern Peruvian Andes and that "it was the identical species of the Uaupés, but under a different name." (90)

The earliest published record of the use of any malpighiaceous narcotic of which I am aware dates from 1858, when Villavicencio (95) reported that the drug was employed by the Záparos, Angateros, Mazanes and other tribes of the upper Río Napo in Amazonian Ecuador for sorcery, witchcraft, prophecy and divination. Although apparently no specimens were taken and no reference to a botanical determination was made in Villavicencio's excellent and complete account, which included a report on self-intoxication, the common name *ayahuasca* was used, and the plant was described as a liana. Later work has definitely shown that *ayahuasca* in Peru and Ecuador belongs, in great part, at least, to the same genus as the Brazilian *caapi*. Indeed, as Spruce noted, although "of the plant itself" Villavicencio "could tell no more than that it was a liana or vine," his "account of its properties" coincided "wonderfully with what I had previously learnt in Brazil." (90)

In a list of plant names in the Tupi language of Brazil, the explorer von Martius (98,99) discussed *caapi*, stating that the Indians of the Rio Uaupés prepared from the fruits of the *caapi* plant an intoxicating drink, which they employed in their dance-ceremonies, and identifying it as *Banisteriopsis Caapi*. Since von Martius had never visited the Rio Uaupés, this report must be accepted as an indirect one. He may have seen specimens of the *caapi* sent by Spruce to Europe and knew that Spruce had reported them as the source of the narcotic beverage. The statement that the fruits of the liana are used as the source of the intoxicants must be read with extreme reservation, even with doubt; for none of the reports of travellers and explorers who have seen the plant in use mention the fruits as the part of the plant employed.

The few incidental references to *caapi* or *ayahuasca*

found in travel books have almost invariably neglected the fundamental question of the botanical identity of the source of the narcotic.

Orton, who travelled widely in the Andes in the last half of the last century, reported (61) the narcotic use of *ayahuasca* amongst the Záparos of the eastern slope of the Andes of Ecuador, but he failed to shed any light on the botanical source of the drug.

Writing on his travels in South America, Crévaux reported (15) that, in southeastern Colombia, the Correguahes of the Río Caquetá prepared an intoxicating beverage from the bark of a plant called *yajé*. He likewise noted, as had Spruce, the use by the Guahibos inhabiting the Río Inírida of Colombia of an intoxicating drink prepared from a root called *capi*, apparently unaware that this *capi* and the *yajé* were probably botanically the same. Many years passed before it was known that *yajé* and *ayahuasca* referred to the same intoxicant.

This report by Crévaux injected a new uncertainty into the picture. Was *yajé* from the same source as *ayahuasca* and *caapi*, or was it made from a different plant? Although, as time went on, the belief that the three were at least generically identical became stronger, the problem was not subjected to careful study until the late 1920's.

In 1866, Simson reported (89) that the Piojes of Ecuador, like their neighbors, the Záparos, "drink *ayahuasca* mixed with *yajé*, *sameruja* leaves and *guanto* wood, an indulgence which usually results in a broil between at least the partakers of the beverage." He failed to identify any of the ingredients botanically, but we may safely assume, I think, that *guanto* refers to a tree-species of *Datura*. This report is, however, of great significance in being apparently the earliest to mention the mixture of a number of elements in preparing the *ayahuasca* drink

and the first intimation that *yajé* and *ayahuasca* might be different plants. In relation to Simson's report that the Záparos mix a number of plant materials to make the narcotic drink, we should point out Spruce's definite statement that, so far as he could discover, the *Banisteriopsis* was used alone by these Indians.

Still a further complication arose when, in 1890, Magelli, a missionary who had spent much time in the Pastaza and Bobonaza areas of Amazonian Ecuador, reported (50) an intoxicating drink which the Jívaro Indians called *natema*. Concerning the botanical source of *natema*, Magelli wrote: "*Natema* is a red bark which, when boiled 24 hours, yields a decoction which deprives those who drink it of their senses for three days . . . ." Magelli seems to have confused *natema* with another narcotic —*maicoma*—which he stated is "a little less toxic than *natema*." It would appear from Magelli's notes that he used the term *natema* to refer to a species of *Datura* and *maicoma* to refer to *ayahuasca*. As Reinburg (69) has suggested, Magelli undoubtedly erred and confused two plants whose uses were very similar. Later workers have established the fact that *natema* is actually referable to *Banisteriopsis*, whereas *maicoma* is, in reality, the much employed tree-*Datura* narcotic of the Jívaros.

Tyler (92) reported, in 1894, the use and preparation of *ayahuasca* by the Záparos of the Río Napo area of Ecuador, stating merely that "the beverage is a decoction of a certain species of liana . . ." and giving a description of the effects of the drug.

Writing of the Colorados of Ecuador in 1905, Rivet (73) referred to *nepi* (*nepe*) as a febrifuge, a violent emetic and an intoxicant and stated that its source was a "liana." Later, in a glossary published in 1907 (74), he identified the Colorado *nepe* and the Cayapa *pinde* as *Banisteriopsis Caapi*. We might here note that a more recent work

EXPLANATION OF THE ILLUSTRATION

PLATE II. BANISTERIOPSIS CAAPI (*Spruce ex Griseb.*) *Morton*. Drawing of a specimen of the type collection. 1, flowering branch, about one half natural size. 2, flower, about two and one half times natural size. 3, fruit, somewhat larger than one half natural size.

Drawn by ELMER W. SMITH

BANISTERIOPSIS *caapi*

(Spruce ex Griseb.) Morton

on these Indians by von Hagen (96) likewise refers the cultivated *nepe* to *Banisteriopsis Caapi*. It is again doubtful that any of these determinations were made on the basis of botanical specimens.

In 1905, Rocha (77) published an account of his trip to the headwaters of the Ríos Caquetá and Putumayo in Colombia and reported that the Inga and Siona Indians of the region, which to-day is included in the Comisaría del Putumayo, employed as a narcotic a "little bush" or "liana" called *yajé*. He stated that the natives would not allow white men to see the plant and that, for this reason, he did not know it from personal observation. His account of its properties, however, coincided very closely with those described for *ayahuasca*, and it was widely assumed that the two were identical.

In 1907, Rivet (75) wrote on the Jívaros of the Ríos Pastaza and Bobonaza in eastern Ecuador. He indicated that they had a narcotic liana which they called *natema* and which he referred to *Banisteriopsis Caapi*. He clearly distinguished between the narcotics *natema* or *yajé* on the one hand and *maicoma* or *maikoa* (*Datura* sp.) on the other. Rivet's identifications were apparently not based on botanical specimens.

Later, Karsten (35) stated his belief that the *ayahuasca* of the Indians of the Ríos Napo, Curaray, Bobonaza and Pastaza; the *natema* of the Jívaros; the *pinde* of the Cayapas; the *nepe* of the Colorados; and the *caapi* of the Rio Negro are all referable to one species: *Banisteriopsis Caapi*. In a letter to Reinburg (69), Karsten reiterated that he had no doubt that *natema*, *ayahuasca*, *nepe* and *pinde* are identical and may be referred to *Banisteriopsis Caapi*, even though he had available no identifications made on the basis of specimens, and that he could not offer a botanical determination of the "*iáhi*" (*yajé?*), an intoxicating liana which the Jivaros never used alone but

always mixed with *natema*. Furthermore, in 1926 (36) and again as recently as 1935 (37), he set forth his belief that *ayahuasca* and *natema* were the same and were referable to *Banisteriopsis Caapi*.

Early in the present century, Koch-Grünberg, whose extensive travels (1903–1905) and investigations in the upper Río Negro basin and in the Apaporis-Caqueta area are classic, stated that "*kaapi*" was prepared from a malpighiaceous shrub (39). I have been unable to find in our herbaria a specimen collected by Koch-Grünberg. Undoubtedly basing his statement on Spruce's earlier work in the same area, he referred the intoxicant to *Banisteriopsis Caapi*. According to Koch-Grünberg (39), the Tukanos of the Vaupés distinguish two species of *caapi;* but for the second he ventured no botanical determination. He also reported that the Karihonas (Hianákoto-Umáua) of the headwaters of the Apaporis knew *Banisteriopsis Caapi*, calling it *yahe* and *hi(d)-yati(d)yahe*. Since he did not penetrate to the sources of this river, he had to assume the "identification" without specimens. He stated, in a letter to Rivet (69) that, for the *yajé* of the Hianákoto and the *mihi* of the Kubeos, he unfortunately did not have botanical knowledge and could not say whether it was *Banisteriopsis Caapi* or some other plant, but that he believed them both to be from this malpighiaceous species.

During his studies amongst the Yekwanas of the upper Orinoco basin of southern Venezuela, Koch-Grünberg (40) found these people using two "species" of narcotic vines, one cultivated and one wild. Both were called *kalí*. The stronger narcotic of the two was the cultivated kind. In his letter to Rivet (69) he stated his belief that these both represented *Banisteriopsis Caapi*.

Hardenberg (28) and Whiffen (100), writing on the Colombian region lying between the Ríos Caquetá and

EXPLANATION OF THE ILLUSTRATION

PLATE III. BANISTERIOPSIS INEBRIANS *Morton*. Drawing of the type specimen. Branch and fruit about one half natural size.

Drawn by ELMER W. SMITH

BANISTERIOPSIS
inebrians Morton
E.W. Smith

Putumayo, inhabited chiefly by Witoto and Bora Indians, definitely reported the use of the narcotics in this area of the northwest Amazon, but neither was able to offer a botanical determination. Hardenberg stated merely that the liana was called *ayahuasca* or *yajé'n;* Whiffen, that it was known as *caapi* north of the Caquetá or *ayahuasca* south of this river. Both of these explorers thus intimated that these sundry names referred to one plant.

In 1917, Safford (83), who had devoted much study to New World narcotic plants, referred both *ayahuasca* and *caapi* to *Banisteriopsis Caapi*, after an evaluation of the literature on the subject.

A suggestion that *ayahuasca* and *yajé* might be different plants, however, can be found in Reinburg's study of the tribes inhabiting the region between the Ríos Napo and Curaray in Perú. In 1921, he wrote (69) that the narcotic drink was an infusion of a few fragments of *ayahuasca*, a liana the diameter of a man's thumb, and leaves of *yajé*, "un petit arbuste, de 1m.50 de haut, á feuilles pétiolées (pétiole de 15 mm.) entiéres, ovales, longues de 20 cm., larges de 7 cm., règuliéres et terminées par une pointe de 2 cm." On the basis of specimens collected, he held that *ayahuasca*, the source of which was always, according to his report, a wild, forest liana, and *caapi* were conspecific and represented *Banisteriopsis Caapi*. Still on the basis of specimens, he suggested that the *yajé* of the Curaray in Peru could, with reservation, be referred to the apocynaceous *Haemadictyon* (approaching, in some respects, *H. amazonicum* Benth.) or a related genus.[1]

It was apparently Spruce (90) who first suggested that

[1] The generic concept *Haemadictyon* has been united with *Prestonia*, and the proper name of the plant to which Reinburg referred is now *Prestonia amazonica* (Benth.) Macbride (47).

Prestonia amazonica might enter into the *caapi* picture.[2] He said that the *caapi-piníma* ("painted *caapi*") is "an apocynaceous twiner of the genus *Haemadictyon*, of which I saw only young shoots, without any flowers. The leaves are of a shining green, painted with the strong, blood-red veins. It is possibly the same species . . . distributed by Mr. Bentham under the name of *Haemadictyon amazonicum* n. sp. It may be the *caapi-piníma* which gives its nauseous taste to the *caapi* . . . and it is probably poisonous . . . , but it is not essential to the narcotic effect of the *Banisteria*, which (so far as I could make out) is used without any admixture by the Guahibos, Záparos and other nations out of the Uaupés."

In 1922, *ayahuasca* or *ayawasca* was reported as a narcotic for the first time from Bolivia, from the Río Beni, by White (101), thus greatly amplifying our knowledge of the range of the use of the intoxicant. White definitely identified it as *Banisteriopsis Caapi*. Although he collected material for chemical analysis, it is not clear from his account whether or not his identification was based on an herbarium specimen. Much of White's botanical material is preserved in the Botanical Museum of Harvard University, but a search through the Eco-

[2] However, Spruce's original field notebook, preserved at the Royal Botanical Gardens at Kew, shows a discrepancy, in this regard, with the published report. The field notes say: "2712. *Banisteria Caapi* Mss. From this is prepared an intoxicating drink known to all the natives on the Uaupés by the name of *caapi*. The lower part of the stem, which is the thickness of the thumb swollen at the joints, is the part used. This is beaten in a mortar with the addition of water and a *small* quantity of the slender roots of the Apocynac. (apparently a *Haemadictyon*) called *caapi-pinima* or painted *caapi*, from its lvs. being stained and veined with red . . . Query? May not the peculiar effects of the *caapi* be owing rather to the roots of the *Haemadictyon* (though in such small quantity) than to the stems of the *Banisteria?* The Indians, however, consider the latter the prime agent, at the same time admitting that the former is an essential ingredient. The two plants are planted near all mallocas (villages) . . ."

nomic Herbarium of Oakes Ames at this institution fails to reveal a specimen of *ayahuasca* collected by White.

In his report, White stated that the intoxicant was prepared either exclusively from the stems of *ayahuasca*, an immense liana with greenish white flowers, or else from *ayahuasca* stems boiled with the leaves of the *chaco*, a shrub with small, globose, red-yellow fruits. Leaves of plants locally called *cagna* and *guayavoche* may also be used with *ayahuasca*, but White could not ascertain whether these were other names for the plant known as *chaco* or whether they represented different species. It is unfortunate that so much uncertainty surrounds White's report, but we may feel rather sure (from the common name *ayahuasca*, from his account of the intoxication and from recent plant collections in adjacent areas) that a species of *Banisteriopsis* is likewise the source of the narcotic in this Bolivian locality.

In several reports, the botanist Rusby, who had accompanied White on the Bolivian expedition, detailed the physiological effects of *caapi* and stated that the drug was derived from *Banisteriopsis Caapi* (80,81,82). In a pharmacological report published in 1924, Seil and Putt (88) reported the isolation from Rusby's material of a "fine powder" with at least three alkaloids (both phenolic and non-phenolic), but they offered no botanical determination for the material which they had studied.

In the same year, 1922, the Belgian botanist-explorer Claes, who had gone to the upper reaches of the Río Caquetá, investigated the *yajé* of the Correguahe Indians of this area of southern Colombia (10). He learned that the *yajé*, hitherto usually described in the literature as "a small bush," was an enormous forest liana. Claes argued—I think quite correctly—that those who had described *yajé* as a small bush had seen young, cultivated individuals and not the vine in its wild state (9).

The intoxicating *yajé* of the Correguahe Indians was made by boiling pieces of the trunk itself together with the crushed bark of the trunk, but later the stem and leaves of a plant which the Indians did not permit him to examine were added to the mixture. This brew produced, as Claes witnessed amongst the natives, very definite narcotic symptoms. It is extremely unfortunate that Claes was unable to procure specimens of the leaves and stems which were used together with the liana, for we now know, from the studies of more recent investigators, that the narcotic *yaje* drink of this region of Colombia is sometimes of a more complex preparation than that of other parts of the Amazon; that very frequently a non-malpighiaceous ingredient may be employed.

Claes did not offer a botanical determination of *yajé* (68). He mentioned that, according to De Wildeman, *yajé* "might be" *Prestonia amazonica*. There is no specimen of this species in the Rijksplantentuin in Brussels, and Claes himself states (68) that he did not obtain material for determining *yajé*, adding: "It thus is necessary to leave for others the task of collecting materials of the definitive classification of the plant." Michiels and Clinquart (54), publishing their observations made during pharmacological experiments with Claes' material, suggested that the stems with which they were working appeared to belong to *Prestonia amazonica*. The French pharmacologist, Rouhier, feeling (although apparently with no sound basis) that *yajé* and *ayahuasca* were one and the same thing, but that they might, physiologically, act differently, put forth the suggestion that *ayahuasca* represents *Banisteriopsis Caapi*, whereas *yajé* could represent the unknown plant which Claes saw the Correguahe Indians add to the brew.

A Colombian chemist, Fischer, was apparently the first to isolate a crystalline alkaloid from *yajé* (22).

Fischer admitted that botanical determination of *yajé* had not been made, but he stated that, to judge from anatomic and histologic details, it seemed to be a species of *Aristolochia*. In 1924, shortly after Fischer's work was done, Rouhier (78) accepted this "identification," stating that his specimens "reminded one of a liana, probably a species of the *Aristolochiaceae*." In a subsequent work, however, Rouhier (79) attributed *ayahuasca* to *Banisteriopsis Caapi* but *yajé* to a "liana," the identification of which was still under discussion. He pointed out that in its physiological action and its geographical range, *yajé* was comparable to *ayahuasca*, and he dismissed its reference to *Prestonia amazonica* as "doubtful." At about the same time, Barriga-Villalba (6), a Colombian chemist, and Albarracín (1), a Colombian pharmacologist, actively investigated *yajé*, but neither shed any further light whatsoever on the botanical identity of the drug. Albarracín described the source of his material as a "climbing shrub" and asserted that the natives did not cultivate *yajé* because it abounded in the forests.

Reporting in 1926 on the *caapi* ceremony of the Tukano Indians of the Río Tikié, a Brazilian affluent of the Uaupés, MacCreagh (49) described the intoxicant as "a thin, almost colorless liquid . . . concocted from the leaves of a vine." He, apparently, failed to collect herbarium material of the vine. It is worthy of note that the Rïo Tikié is the same area where Koch-Grünberg had made his observation on *caapi*. It is very near the locality where Spruce first met with the drug (90). Commenting on "*kaapi*," which he had encountered in his travels in the same general region, the English explorer McGovern (53) failed to venture a botanical determination, merely mentioning that the drug was made from "a root."

A rather inclusive survey of what had been accom-

plished up to that date on the botanical identification and chemical constitution of this complex of malpighiaceous narcotics was published in 1927 by two French pharmacologists, Perrot and Hamet (66,67). They pointed out that even more confusion reigned in the chemical field of investigation than in the botanical, principally because pharmacologists and chemists consistently disregarded taxonomic accuracy in identifying the sources of plant materials under study. Perrot and Hamet concluded that (a) *yajé*, *ayahuasca* and *caapi* refer to one species of plant: i.e., *Banisteriopsis Caapi;* and that (b) no apocynaceous plant is at all concerned in the problem of the source of the narcotic known under these three names. Notwithstanding the meritorious efforts of Perrot and Hamet, their review brought little clarification into either the botanical or the chemical picture.

In reply to the article by Perrot and Hamet, the German botanist Niedenzu (59) published several very interesting observations based on herbarium specimens preserved in the Berlin Herbarium. These specimens are, of course, no longer extant, but the notes are of special importance because of the authenticity of the determinations at the hand of an outstanding specialist in the *Malpighiaceae*. The collection *Tessmann 5424* from Yarina Cocha on the Río Ucayali in eastern Peru represented, according to Niedenzu, a mixture: leaves of *Mascagnia psilophylla* (Juss.) Griseb. var. *antifebrilis* (Ruíz & Pav.) Ndz. and, in a paquet attached to the sheet, samaras of *Banisteriopsis quitensis* (Ndz.) Morton; on the label was annotated the vernacular name of *hayawasca* or *ayawasca* and the observation "Stücke der Liane gekocht, dann kalt genommen." Niedenzu further called attention to three specimens of *Banisteriopsis quitensis*. *Eggers 15485*, from eastern Ecuador, consisted of leaves, scanty flowers and plentiful fruit and had a note that,

from the stems, an intoxicating brew was prepared. Niedenzu stated that the characters of *Eggers 15485* did not seem to correspond very closely with *Banisteriopsis quitensis* as it was described. *Tessmann 4974* and *5325*, from the Ríos Pastaza and Itaya, respectively, were referred without question to *Banisteriopsis quitensis*. Both were called *ayawasca* and were reported to be the source of a narcotic drink employed by witch-doctors. Tessmann identified *Tessmann 5325* as *Banisteriopsis Caapi*, but Niedenzu pointed out that the collection was distinct from this species. In summary, Niedenzu stated that these wild and cultivated plants of *Banisteriopsis* from eastern Ecuador and Peru and the uses reported for them would seem to indicate that yageine, the alkaloid whose source was still in doubt, might well have come from similar species and that, on the basis of his studies, it would seem that three sources of the narcotic "*ayawasca*" ought to be considered: *Haseagnia psilophylla* var. *antifebrilis*, *Banisteriopsis quitensis* and *B. Caapi*.

Another attempt to put some order into the confusion resulting from field observations and fragmentary specimens occasionally gathered by ethnologists was made by Gagnepain, who, in 1930, published his botanical opinions relative to these narcotics (24). He pointed out (a) that, according to Reinburg, *ayahuasca* was "probably" *Banisteriopsis Caapi*, but that *yajé* could not be referable to this species; (b) that *yajé* seemed to approach *Prestonia amazonica;* (c) that fragments received as *yajé* by the chemist Rouhier in 1924 showed the plant to be an "opposite-leaved vine"; (d) that both Rivet and Reinburg sent in material which seemed to represent the same malpighiaceous plant. Later, Gagnepain received, through Rouhier, a specimen from the Departamento de El Valle in Colombia, where the plant was cultivated under the name of *yajé*. The specimen, with leaves and

inflorescence attached, was determined as *Banisteriopsis Caapi*. This led Gagnepain to the rather extraordinary assertion that the *yajé* of Colombia was the same species as the *caapi* of Brazil, but different from the *yajé* of Ecuador. He could state with assurance only that the Ecuadorian *yajé* represented a species of *Banisteria* "near *ferruginea*" and that an exact clarification of the botanical sources of *yajé* was still far from realization.

In 1929 and 1930, the Russian botanist Hammerman (26,27) published a rather complete survey of the problem. His statements were founded on an evaluation of reports in the literature in the light of a study of material gathered in 1925–1926 by G. N. Varonof and S. V. Juzepczuk along the Río Orteguaza, in the Colombian Comisaría del Caquetá. Pointing out that Zerda Bayón's assertion that the Indians of the Caquetá mixed four kinds of leaves to make a brew which they called *yajé*, Hammerman indicated that the material of Voronof and Juzepczuk gave a variety of results when chemically analyzed. He further stated that there seemed to be several species of *Banisteriopsis* involved, even though most of his material apparently was referable to *Banisteriopsis quitensis*. Any one of the species could be a source of the narcotic preparations of the Indians. He was, withal, careful to emphasize that only Spruce had seen in flower an actual vine definitely known to be used to make the hallucinating drink. He intimated that the known variation in preparation, use and effect of the narcotics called *caapi*, *yajé* and *ayahuasca* might be due to differences in composition.

In 1931, Morton (58) described a new species of *Banisteriopsis* from southern Colombia, naming it *B. inebrians* Morton because of its use by the Indians of the Comisaría del Putumayo as an inebriant. Basing his statements on the meticulous field observations of the late Guillermo Klug, a German plant collector who worked

in eastern Peru and adjacent parts of Colombia, Morton indicated that at least three species are employed in this region: *Banisteriopsis Caapi*, *B.inebrians* and *B.quitensis;* and that *Banisteria longialata* Ruiz ex Ndz. and *Banisteriopsis Rusbyana* (Ndz.) Morton may enter certain of the narcotic preparations as additional ingredients.

Several reports on chemical studies of *caapi* published during the late 1920's and the 1930's considered the botanical identification of the intoxicant under investigation.

Reutter, reporting in 1927 (72) that he had isolated yageine and yagenine from the vegetal parts of *yajé* or *ayahuasca*, accepted Rouhier's "identification" as *Prestonia amazonica*, stating that some tribes add to their *yajé* drink *Banisteriopsis Caapi* or "*Datura arborea* L." Lewin, a year later (44), wrote that *ayahuasca* was "a member of the *Malpighiaceae.*"

In 1929, Keller and Gottauf (38) worked with material of *ayahuasca* from Bolivia and Peru, referring it to "a *Banisteria,*" (although they had no leaves nor flowers available) and isolated a harmine-like alkaloid.

Costa and Faria (13,14) held that *yajé*, *ayahuasca* and *caapi* were the same narcotic and were derived from *Banisteriopsis Caapi.* Three years later, Chen and Chen (8) summarized briefly the literature references and indicated their belief that *caapi*, *yajé* and *ayahuasca* represented *Banisteriopsis Caapi*, "a woody climber that attains a height of 3 to 4 metres and attaches itself to the trunks of large trees" or that is "grown in the North-western regions of South America." Chen and Chen identified the alkaloids telepathine, yajeine and banisterine with harmine from *Peganum Harmala*, corroborating experimentally the earlier suggestions of Wolfe and Rumpf (104). The real importance of Chen and Chen's paper, however, lies in the chemical study, apparently for the

first time, of vegetal material which seems to have been identified on the basis of botanical specimens. For the "twigs, leaves and roots of *caapi*" and the "decoction just as used by the Indians" which were subjected to chemical analysis had been collected by the botanist Williams near Iquitos, Peru, and were determined as *Banisteriopsis Caapi* (4,102,103).

For the most part, recent investigators who have devoted critical attention to the study of the South American malpighiaceous narcotics have concurred with Hammerman, Gagnepain and Klug that several species of *Banisteriopsis*, if not of other genera, may be involved in some regions (12).

Nevertheless, some contemporary writers tend to simplify the problem of identification, even though their "determinations" are seldom, if ever, based on specimens. While they are certainly not specialists, they are often quoted uncritically in technical works. Some, as in the case of Reko (70,71), have stated that *ayahuasca*, *pinde*, *natema*, *caapi* and *yajé* are all derived from *Banisteriopsis Caapi*.

In his dictionary of Amazonian plant names, Le Cointe (41) indicated a belief that *ayahuasca* and *caapi* were *Banisteriopsis Caapi* and that *yajé* corresponded to "another plant that enters into the composition of the *caapi*-drink as prepared by some tribes," and he pointed out that some writers identify *yajé* as *Prestonia amazonica*. Von Hagen (96,97) considers both *natema* and *caapi* to be *Banisteriopsis Caapi*.

In 1936, Pardal (62) referred *caapi* to *Banisteriopsis Caapi* and *yajé* to *Prestonia amazonica*. The following year, however, he stated (63) that *caapi*, *yajé* and *ayahuasca* are *Banisteriopsis Caapi*. Maxwell (52), after an evaluation of the literature concerning the identity of *caapi*, concluded that the narcotic was a species of *Ban-*

isteriopsis, that "other vegetable ingredients are sometimes included in the making of the beverage" and that their identity is still in question.

Lewin (42,45,46) identified *natema*, *yagé*, *yahé*, *nepe*, "*kahi*" and *pinde* as *Banisteriopsis Caapi* and enumerated the following Indian tribes as "addicted" to the use of this narcotic species: Guahibo, Tukano, Correguahe, Tama, Záparo, Vaupé, Yekwana, Baré, Baniva, Mandawake, Tariana, Siona, Jívaros, Colorados and Cayapas. Although Lewin held the principal ingredient to be *Banisteriopsis Caapi*, he admitted that it was sometimes used together with other plants. Amongst these plants, he named, as one possibility, *Prestonia amazonica* (43), although he strongly doubted that the name *yajé* referred exclusively to *Prestonia amazonica*. He further indicated that some Indians probably also add tobacco-water to the beverage.

A most interesting note on *ayahuasca* in Peru appeared in 1943 (94) and included a "recipe" for making the intoxicating beverage. Unfortunately, all of the plants employed were indicated with Indian names, with no hint as to their identity. The recipe commonly used in the vicinity of Iquitos has, as its principal ingredient, the liana or "death vine," *ayahuasca*, which is undoubtedly a *Banisteriopsis*. Into the decoction of this vine, the leaves of a species of *muémueti* are put; the name *muémueti* is said to refer to several plants, only one of which is used at a time. According to this account, the *muémueti* is responsible for the visual hallucinations. Also employed in the decoction is an evil-tasting tuber called *katija*. To sweeten up the *ayahuasca* drink, leaves and seeds of a plant known as *pujana* are added.

Herrera (31) listed the *ayahuasca* of Valle de Lares as *Banisteriopsis metallicolor* (A. Juss.) O'Donnell & Lourteig and reported it as a "planta tóxica."

Caller (7), in a consideration of the historical literature on the botanical sources of *ayahuasca*, concluded that the species used to prepare this narcotic drink is *Banisteriopsis Caapi* and that *B. quitensis* is a synonym of *B. Caapi*. Other recent writers on Peru (18,97) attribute *ayahuasca* exclusively to *Banisteriopsis Caapi*.

Padre Plácido, who spent many years as a missionary in the Putumayo of Colombia, did not identify *yajé* botanically (17), but he stated that the Sionas often add to the narcotic drink of this name the *pęji* or *yakoborrachero*—the *floripondio* of Mocoa, or, probably, *Datura suaveolens* H. & B. ex Willd.

Sandeman (84) mentioned *yajé* casually, attributing it to *Prestonia amazonica*.

Allen (2), in an excellent description of the *yurupará* ceremony of the Kubeo Indians of the Río Vaupés in Colombia, indicated *Banisteriopsis Caapi* as the source of the narcotic beverage upon which this frenzied ritual is based. Taylor (91), following Allen, has attributed the malpighiaceous narcotics to *Banisteriopsis Caapi*.

In a recent and authoritative work on plant alkaloids, Henry (30) identified the narcotics known as *yajé*, *caapi* and *ayahuasca* as *Banisteriopsis Caapi*, *B. metallicolor* or *Banisteria lutea* Ruíz ex Griseb.

Manske and Holmes (51) attributed all three to *Banisteriopsis Caapi*. In 1946, Ducke (20) identified the famous narcotic of the natives of the extreme northwest of the Amazon Valley, called *caapi* in the Brazilian part and *yagé* in the Colombian part of the region, as *Banisteriopsis Caapi*. Hesse (32) attributed *ayahuasca* and *yajé* both to *Banisteriopsis Caapi*, and Möller (55) stated that *caapi* was exclusively referable to this species.

Recently, Macbride (48), probably following Morton (58), pointed to *Banisteriopsis Caapi*, *B. inebrians* and *B. quitensis* as the principal sources of the alkaloid vari-

EXPLANATION OF THE ILLUSTRATION

PLATE IV. BANISTERIOPSIS CAAPI (*Spruce ex Griseb.*) *Morton*. Photograph of the plant from which the collection *Schultes & Cabrera 13156a* was made.

Photograph by HERNANDO GARCÍA-BARRIGA

Plate IV

EXPLANATION OF THE ILLUSTRATION

PLATE V. Cultivation of *Banisteriopsis Caapi* (Spruce ex Griseb.) Morton (*Schultes & Cabrera 17209*) by the Barasana Indians in the headwaters of the Río Piraparaná, Comisaría del Vaupés, Colombia.

Photograph by RICHARD EVANS SCHULTES

Plate V

ously known as telepathine, yageine or banisterine. He stated, however, that it might also be found in "a number of related plants or forms" and quoted Morton in citing *Banisteriopsis Rusbyana* and *Banisteria longialata* as admixtures known by the names of *oco-yagé* and *chagro panga*.

O'Connell and Lynn (60), working on material of *Banisteriopsis inebrians* from the Putumayo of Colombia, found that the stems contain harmine and the leaves "an alkaloid which was partly identified as harmine." The work of O'Connell and Lynn is noteworthy as representing apparently the second chemical investigation carried out on material of *Banisteriopsis* identified through herbarium material.

Mors and Zaltzman published a most interesting contribution in 1954 (56) in which they indicated their opinion, based on chemical examination, that yageine was different from harmine. On the basis of a brief review of the literature, they concluded that *caapi* and *ayahuasca* were referable to *Banisteriopsis Caapi* but that *yagé* was not the same narcotic.

Most recently, Fabre (21) published an historical review of *caapi*, *ayahuasca* and *yajé*, indicating his belief that only one species—*Banisteriopsis Caapi*—is the source of these narcotics, though citing Spruce that, amongst certain tribes, another plant may oftentimes be added in the preparation of the narcotic drink.

IV

Although Morton (57) has convincingly shown why the generic epithet *Banisteria* is not available for the group of malpighiaceous plants which should be called *Banisteriopsis*, in accordance with the lucid arguments of Robinson (76), there is a tendency to persist in the incorrect use of the name *Banisteria*. This tendency is

not always attributable to ignorance or uncertainty. It is frequently the result of a deliberate flouting of the International Rules of Botanical Nomenclature. Its continuation will not lead to standardization or to clarity but to the further beclouding of the exact identity of the malpighiaceous narcotics as well as to confusion in taxonomic and floristic works.

Ducke (19,20), in refusing to use the generic epithet *Banisteriopsis*, stated that his reason was an objection to the multiplication of names in botany. Macbride (48) not only chose to use *Banisteria;* he made the new combination *Banisteria inebrians*, attributing it erroneously[3] to Morton who has been most outspoken against this use of the name *Banisteria*. And recently Baldwin, in an article on the chromosomes of *Banisteriopsis Caapi* (5) chose to use the epithet *Banisteria*.

Non-botanical writers, faced with this lack of standardization in technical papers, often continue to use *Banisteria* instead of *Banisteriopsis* in connection with the narcotic species under discussion (21,30,32,46,51,62,63, 64,91).

An increasing number of technical writers, nevertheless, are employing the correct generic epithet (12,23, 33,34,65,85,93).

V

Although little new information has been published since 1931, a study of material preserved in our herbaria and museums, and recent field observations and collections by several plant explorers have contributed other data which should be made available. It would seem to be especially necessary to do this, since, as the foregoing literature review has shown, little if anything of an ac-

[3] "*Banisteria inebrians* Morton, Journ. Wash. Acad. Sci. 21: 485 (1931)."

curate nature may be looked for from the usual type of anthropological field investigation.

In utilizing data found on herbarium labels, caution must be taken. For a field botanist might jot down "used as a narcotic" on the basis of information supplied by a native and without sufficient checking or without himself having seen the plant thus employed. Nevertheless, such data may be of great value as an orientation in problems as complex as the one at hand.

A further drawback—and a serious one—to the use of sterile specimens for botanical identification is the difficulty, in a genus of such vegetatively similar species, of arriving at a satisfactory determination.

Usually, all we have to work with in studying the malpighiaceous narcotics is sterile material. The cultivated plants seem rarely or never to flower (probably because of constant cutting back), and the forest lianas blossom sporadically and are seldom found in flower by collectors. In one hundred years, for example, we have only one flowering collection of *Banisteriopsis Caapi* from the field (that is, excluding plants brought to flower in experiment stations or botanical gardens), and that is the type collection made by Spruce. My determinations of most of the older specimens concur closely with the identifications made by Dr. C. V. Morton, who specialized in the *Malpighiaceae*. I have identified the numerous sterile herbarium specimens considered below with reserve, even though I have put in more than ten years of field study on the problem. As the result of prolonged study of living plants, one acquires some familiarity with certain of the variations which these species may show under different natural habitats. But I must further point out that this long period of field study in itself has made me rather cautious about drawing categorical and far-reaching conclusions from what herbarium material we have at hand

at the present time. No one can feel more certain than I that we are just beginning our serious taxonomic studies of the complex of malpighiaceous narcotics.

Perhaps the most revealing observation based on botanical material to have been made since Spruce's time has not hitherto been published. I was fortunate in discovering in the Museum of Economic Botany at the Royal Botanic Gardens at Kew several samples of the "*yajé* plant," comprising twigs and leaves (Econ. Mus. Kew 60 1913) from the Caquetá, Colombia. These were sent in 1913 by Percy E. Wyndham, Esq., His Majesty's Minister in Bogotá. The leaves were determined by Dr. T. A. Sprague who wrote, in a communication attached to the specimens, that they represented species of *Malpighiaceae* (possibly *Tetrapterys*) and that "the twigs no doubt belonged to one of them." I have carefully compared the leaves with specimens of the *Malpighiaceae* at Kew and would agree (insofar as it is possible to determine such limited sterile material) with Sprague that they may be referable to *Tetrapterys*. This is the first time that a malpighiaceous genus other than *Banisteriopsis* has been mentioned as the source of a narcotic.

With the Wyndham material at Kew, there are several communications concerning the specimens. It is apparent that Wyndham was moved to gather specimens of the *yajé* plant as the result of interest aroused by a newspaper article (3). This article spoke rather optimistically of *yajé* as a cure for beri-beri, and it published a long letter from Dr. Rafael Zerda Bayón, a Colombian pharmacist, who put forth extraordinary claims concerning the telepathic properties of the vine. No botanical determination was offered. Sprague, in one of the communications with the Kew specimens, wrote: ". . . Dr. R. Z. Bayón says he has deposited specimens of the

'Bejuco de *Yagé*' with the Ministry of Public Works and that he doesn't think it desirable to send the specimens abroad! Apparently, the climber has not been identified."

The collection *Killip & Smith 27385*, from Iquitos, Peru, represents *Banisteriopsis Caapi* and reports the following information: "Ayahuasca. Woody vine. Strong narcotic tea brewed from the leaves and stem produces fanciful dreams; also used as a cure for many diseases and as an intoxicating beverage." *Killip & Smith 29486* and *29825*, from the same region, likewise represent *Banisteriopsis Caapi*, but in connection with these two collections, the botanists made no notes as to their uses. *Ducke 25258* is a flowering collection of *Banisteriopsis Caapi* from a plant gathered in Amazonian Peru and cultivated in the Jardím Botánico in Rio de Janeiro. *Williams 3741* and *8224*, also from the Iquitos area, likewise are referable to *Banisteriopsis Caapi*, and are the basis of Williams' report (103) that "the lower part of the stem and its leaves are crushed and boiled in water. When sufficiently triturated, the infusion is passed through a sieve to remove fibrous material, and to the residue water is added to render it drinkable. The resulting greenish-brown infusion has a disagreeable, bitter taste and is said to contain narcotic properties."

From this wealth of material, we may judge that *Banisteriopsis Caapi* is rather commonly cultivated in Amazonian Peru. Still another collection, *Seibert 2173* (also from the Amazonian basin of Peru but from the Río Tahuamanú in the Madre de Dios, far from the Iquitos area) has been determined as *Banisteriopsis Caapi*, even though its leaves are slightly atypical, due possibly to the fact that the plant was a wild liana in the jungle and not a cultivated shrub in open gardens. The collector reported: "*Ayahuasca.* Liana in forest. Infusion taken

internally and preparation from bark produces illusions. Used by Indians. Narcotic."

It is from the Amazonian regions of Colombia, however, that the greatest number of collections of the malpighiaceous drugs has recently been taken. *Klug 1971* and *Cuatrecasas 10597*, both from the Comisaría del Putumayo, represent apparently ***Banisteriopsis Rusbyana***, a species usually characterized by large leaves. The former collection, from the village of Umbria, is reported to be called "*chagro-panga* or *oco-yagé*"; the latter, from near Puerto Ospina on the Río Putumayo, is known amongst the natives as *yageúco* (undoubtedly the same as *oco-yagé*) and is reputedly cultivated by the Kofán Indians who use the leaves in the preparation of the narcotic *yajé*. In 1953, I collected what appears to be ***Banisteriopsis Rusbyana*** near Mocoa, capital town of the Putumayo, under the name *chagropanga;* the leaves of this plant are reputedly used together with the pounded bark of ***B.*** *inebrians* in the preparation of the drink *yajé*.

In 1931, Klug discovered in Umbria what turned out to be an undescribed species of ***Banisteriopsis***. Described by Morton (58) as ***Banisteriopsis*** *inebrians*, this forest liana, which grows to a length of ninety feet, goes under the epithet of *yagé del monte* amongst the Ingano Indians of the Putumayo. Klug collected ample botanical material of the *yagé del monte* and observed (58): "One of the most interesting plants found in the region of the upper courses of the Ríos Putumayo and Caquetá is the *yagé*. The Indians make a beverage of either the wild or cultivated *yagé*, boiling it in a large earthenware vessel an entire day, until there is formed a sort of liquid, like the syrup of sugar cane. They add to the *yagé* the leaves and the young shoots of the branches of the *oco-yagé* or *chagro-panga* (No. 1971), and it is the addition of this plant which produces the 'bluish aureole' of their visions."

More recently, *Banisteriopsis inebrians* has been reported as the source of a narcotic in the same region. *Cuatrecasas 10598*, collected near Puerto Ospina, apparently represents this species and is cultivated under the name *yagé* by the Indians as the "principal ingredient" of the narcotic drink, the unboiled stem ("tallo crudo") being employed. Likewise, *Cuatrecasas 11061* was taken from a plant cultivated by the Kofán Indians of the nearby Río Sucumbíos. In 1942, I found the same Indians using cultivated *Banisteriopsis inebrians*, called *oofíi* in the Kofán language, as the source of a narcotic drink at Puerto Ospina and on the Sucumbíos, and I experimented in both localities with the intoxicant prepared from vines from which the collections *Schultes 3452* (from a cultivated plant) and *3474* (from a wild liana) were made. The collection *Schultes 3346*, likewise apparently referable to *Banisteriopsis inebrians*, was taken from a vine pointed out by the Ingano Indians of Puerto Limón on the nearby Río Caquetá as the plant from which, without admixture, they prepare their *yajé*. From Mocoa, capital town of the Putumayo and centre of the Inganos, still other collections of *Banisteriopsis inebrians* were made (*Schultes & Smith 3037*; *Schultes & Cabrera 19113*) with the field annotations that they were called *ayahuasca* or *yajé* and *bejuco de oro* ("golden vine"), that they were narcotic and that the leaves were used as a strong purgative. I have found *Banisteriopsis inebrians* to be used with and without the admixture of any other species of the genus, but decoctions of this species had marked narcotic effects each time I drank them, whether or not any admixtures had been used.

What is probably *Banisteriopsis quitensis* was reported by Klug (*Klug 1934*) as *yagé cultivado* (58) in the Umbria region. Later, Cuatrecasas (*Cuatrecasas 10599*) noted that the Kofáns near Puerto Ospina grow this spe-

cies and use it in the preparation of the intoxicating *yajé* drink. He stated that the plant material is boiled to prepare the beverage. Notes with the collection *García-Barriga 4634a*, which has been identified as probably referable to this same species, indicate that the Indians who live between Mocoa and Umbria (Inganos) call the vine *yajé* and prepare an intoxicant from it, with the admixture of two other plants. García-Barriga (25) stated that *Banisteriopsis quitensis* is "cultivated near their dwellings in order to have it at hand during the rainy season" and that "they make with the stems a drink or beverage which they call *yaje*." One of the admixtures, according to García-Barriga, is the amaranthaceous *Alternanthera Lehmanii* Hieron., locally known as *borracha* or *chicha* (both of which terms refer to "intoxicant" in Spanish); the other admixture could not be determined. *Alternanthera Lehmanii* is said by García-Barriga to be added also to native beers or *chichas* as a condiment to increase their intoxicating properties. A sterile collection which seems to represent *Banisteriopsis quitensis* (*Pérez-Arbeláez 639*) was stated to be used in the region of Florencia on the Río Orteguaza in preparing an inebriating drink. Williams (103) has reported *Banisteriopsis quitensis* to be used in the same way as *B. Caapi* in Amazonian Peru, where it is gathered from both wild and cultivated plants.

The Indians of the Comisaría del Vaupés in Amazonian Colombia have conserved many of their aboriginal customs, such as the use of the malpighiaceous narcotics. Unlike the natives of the Putumayo, at the eastern foothills of the Andes, who use species of *Banisteriopsis* in a concentrated decoction made by boiling the plant material, the Indians of the Vaupés prepare a cold-water infusion of the bark. *Banisteriopsis quitensis* and *B. inebrians* seems to be lacking in the flora of the Vaupés,

but *B. Caapi* and what appears to represent *B. Rusbyana* are cultivated for use as intoxicants. The collections cited below are all sterile and identification is, therefore, not certain, but, in each case, they were taken from plant material which I know, from personal experimentation, to possess narcotic properties.

The Taiwano and Kabuyarí Indians of the Río Kanamarí, an affluent of the middle course of the Apaporis, prepare their *kahcé* from two kinds of *Banisteriopsis*, both cultivated. One vine had no leaves at the time of the Baile de la Sabaleta, when *yajé* is drunk, but the stems obviously belonged to a species of *Banisteriopsis*. The other is represented by the collection *Schultes & Cabrera 13156a* and corresponds in all vegetative characters with *Banisteriopsis Caapi*.

Those Makunas who live along the Río Popeyacá, also an affluent of the Apaporis, prepare the drink in two ways: either with one species of *Banisteriopsis* or with two species of this genus, both cultivated. The drink is called *kahcé* by the Makunas. When it is made from one species, *Banisteriopsis Caapi* (represented by *Schultes & Cabrera 15587*) is employed: this species is known in Makuna by the name *reé-ma*. When two species are used in the preparation of the drink, *Banisteriopsis Caapi* is mixed with a vine called *me-ne-ka-heé-ma* ("vine of *ka-heé*") and referable probably to *B. Rusbyana* (*Schultes & Cabrera 15588*). Of *Banisteriopsis Caapi*, only the rasped bark is employed, but of *B. Rusbyana* either the leaves or the bark or both are utilized. With these natives, I took *yajé* twice; once made with bark from *Schultes & Cabrera 15587* and leaves from *Schultes & Cabrera 15588*, and once with bark of *Schultes & Cabrera 15587* alone. Intoxication was induced in both cases, and I was unable to note that one preparation had different or stronger effects than the other. Both of these

preparations are taken by all men of the tribe during dances. When the medicine-man employs the narcotic for purposes of diagnosis or to enable him to work evil on others, he takes a strong preparation of *Banisteriopsis Caapi* alone. The Makunas of the Popeyacá report that, in difficult cases of diagnosis, the medicine man will add a few crushed leaves of a tree which is abundant along the flood-banks of the river: *guay-ee-ga-mó-yoo-ke-reé* ("tree of the gill of fishes"). This tree, represented by *Schultes & Cabrera 15556*, has been determined by Dr. R. W. Woodson as probably *Malouetia Tamaquarina*. The leaves contain an abundance of sticky, white latex and, as the species belongs to the *Apocynaceae*, possibly are poisonous in large doses. Indeed, there are persistent reports in the upper Amazon that the bones of the *pajuíl* are, at the time when *Malouetia Tamaquarina* sets fruit (which this bird is said to eat), highly poisonous to dogs which may eat them (86). I have never witnessed the use of *Malouetia* and was not able to corroborate the report with those who understand the properties of medicinal plants either amongst the Makunas or neighboring peoples.

The Indians of the headwaters of the Río Piraparaná cultivate *caapi* in almost every plot around their houses. *Schultes & Cabrera 17209* from a Barasana Indian site on the Caño Teemeeña represents *Banisteriopsis Caapi*. A cold-water infusion of the rasped bark of this plant to which was added water in which dried tobacco leaves (*Nicotiana Tabacum* L.) had been steeped had highly narcotic effects.

Banisteriopsis Caapi is apparently the commonest source of the narcotic *caapi* drink in adjacent parts of Brazil. It was from Ipanoré on the Rio Uaupés near the Colombian boundary that Spruce collected the type specimen of this species. A recent collection, *Duke 153*,

taken from a plant cultivated in Manáos from material gathered along the Rio Curicuriarí, an affluent of the upper Rio Negro, represents *Banisteriopsis Caapi*.

During a year's stay in the upper Rio Negro and its affluents in Brazil in 1947, I heard, on several occasions, reference to two kinds of *caapi*. As has been pointed out in detail above, it was from this region that Spruce reported a second kind of *caapi*, known locally as *caapi-pinima*, which he suggested might be referable to the apocynaceous vine *Prestonia amazonica* (*Haemadictyon amazonicum*). And it was likewise in this region that Koch-Grünberg found that the Tukanos distinguish two species of *caapi*, for only one of which (*Banisteriopsis Caapi*) he ventured a determination.

It was my good fortune in 1948 to be able to witness the preparation of and to take a narcotic drink amongst the nomadic Makú Indians of the Ira-Igarapé, an affluent of the Rio Tikié which flows into the Rio Negro below Ipanoré. Specimens (*Schultes & Lopez 10184*) taken from the flowering vine, from the bark of which a cold-water infusion was made without the admixture of other plants, were found to represent an undescribed species of a malpighiaceous genus allied to *Banisteriopsis*— *Tetrapterys methystica* R. E. Schultes (87). The beverage prepared from *Tetrapterys methystica* has a yellowish hue, quite unlike the coffee-brown color characteristic of all preparations of *Banisteriopsis* which I have seen or taken. A small amount of stem material for chemical study which I gathered from this wild vine was lost in the overturning of my canoe, so nothing, unfortunately, can be stated concerning the chemical nature of the plant. Two important points, however, should be emphasized in connection with this discovery: (1) *Tetrapterys methystica* may possibly represent the second kind of *caapi* reported by Spruce and Koch-Grünberg, and it might be that the

epithet *caapi-piníma* ("painted caapi") alludes not to "painted leaves but to the unusual yellowish hue of the drink prepared from it; and (2) the tentative identification as "possibly *Tetrapterys*" of the sterile material sent to Kew by Wyndham from the Caquetá of Colombia would seem to be strengthened by the employment, even at such a distance, of a species of *Tetrapterys* in the elaboration of a drink with proven narcotic properties.

Summary

1. The narcotic drink known in the western Amazonian regions as *caapi* (Brazil and Colombia), *yajé* (Colombia) and *ayahuasca* (Ecuador, Peru and Bolivia) is made basically from the same or closely related plants of the *Malpighiaceae*. It is probable that the Indian names *natema*, *nepe* and *pinde* are synonymous with the three more commonly used names mentioned above.

2. The most widely employed species are members of the genus *Banisteriopsis*. The species most frequently used in Brazil, easternmost Colombia and much of the Amazon basin of Peru and Bolivia is *Banisteriopsis Caapi*, but *B. Rusbyana* seems also to be utilized in easternmost Colombia. In the westernmost fringe of the Amazon basin, along the Andean foothills of Colombia, Ecuador and Peru, *Banisteriopsis quitensis*, *B. inebrians* and *B. Rusbyana* seem to be the species most preferred.

3. The closely related genus *Tetrapterys* is employed in Brazil and possibly in Colombia. The only species of *Tetrapterys* definitely identified as the source of the narcotic *caapi* is *T. methystica*.

4. *Mascagnia psilophylla* var. *antifebrilis* has been indicated as one possible source of *ayahuasca*, but this report is open to very serious doubt.

5. The identification of *yajé* as a species of *Aristolochia* is definitely without foundation.

6. *Prestonia amazonica* (*Haemadictyon amazonicum*) of the *Apocynaceae* has frequently been named as the source of *yajé* and *caapi*. There is little or no reliable evidence that this vine is ever employed, at least as the prime ingredient, in preparing the narcotic drink.

7. The species of *Banisteriopsis* and *Tetrapterys* are known to be employed alone and to have narcotic properties when thus used. Two species of *Banisteriopsis* may also occasionally be utilized together.

8. Non-malpighiaceous plants are known occasionally, but apparently not frequently, to be added as admixtures together with *Banisteriopsis* in some areas. *Prestonia amazonica* has been reported to be thus used in Brazil. The solanaceous *Datura* and the amaranthaceous *Alternanthera Lehmanii* have been indicated as an added ingredient in Colombia. The apocynaceous *Malouetia Tamaquarina* may enter into the preparation of the narcotic in the Vaupés of Colombia, but this report could not be verified. Several unidentified plants have been mentioned as admixtures in Bolivia, Colombia and Peru.

EXPLANATION OF THE ILLUSTRATION

PLATE VI. (*Upper*). Makuna Indian witch-doctor gathering stems of *Banisteriopsis Caapi* (Spruce ex Griseb.) Morton (*Schultes & Cabrera 15587*) for preparation of narcotic drink. Río Popeyacá, Comisaría del Amazonas, Colombia.

(*Lower*). *Banisteriopsis inebrians* Morton (*Schultes & Cabrera 19113*) cultivated in an Indian garden near Mocoa, Comisaría del Putumayo, Colombia. The rasped bark of this plant, which is referred to as *yajé*, is added to the leaves of *Banisteriopsis Rusbyana* in the preparation of the narcotic drink.

Photographs by RICHARD EVANS SCHULTES

Plate VI

EXPLANATION OF THE ILLUSTRATION

PLATE VII. BANISTERIOPSIS RUSBYANA (*Ndz.*) *Morton* (*Schultes & Cabrera 19112*) growing in secondary forest at Mocoa, Comisaría del Putumayo, Colombia. The leaves of this plant, which is called *chagropanga*, are added to the rasped bark of *Banisteriopsis inebrians* to prepare the *yajé* drink in the Mocoa area.

Photograph by RICHARD EVANS SCHULTES

Plate VII

EXPLANATION OF THE ILLUSTRATION

PLATE VIII. Makuna witch-doctor under the influence of caapi prepared in a cold-water infusion of the bark of *Banisteriopsis Caapi* (Spruce ex Griseb.) Morton (*Schultes & Cabrera 15587*) with no admixtures. Río Popeyacá, Comisaría del Amazonas, Colombia.

Photograph by GUILLERMO CABO O.

Plate VIII

LITERATURE CITED

1. Albarracín, Leopoldo. Contribución al estudio de los alkaloides del *yagé*. [Bogotá] (1925).

2. Allen, Paul H. Indians of southeastern Colombia. Geogr. Rev. 37 (1947) 580.

3. Anonymous. The yajé plant. Times (London) South American Supplement, Aug. 27, 1912.

4. Anonymous. Toxicologist completes study of Peru's "death vine." Field Mus. News 10: no. 3 (1939) 5.

5. Baldwin, J[ohn T.]. Banisteria Caapi Spruce: Its chromosomes. Bull. Torr. Bot. Club 73 (1946) 282.

6. Barriga-Villalba, A. M. Un nuevo alkaloide. Bol. Soc. Col. Cienc. Nat. (1925) 31–36.

7. Caller Ibérico, Clorinda. Ayahuasca. Bol. Mus. Hist. Nat. Javier Prado 5 (1941) 313.

8. Chen, A. L. and K. K. Chen. Harmine, the alkaloid of caapi. Quart. Journ. Pharm. & Pharmacol. 12 (1939) 30.

9. Claes, Florent. Quelques renseignements sur les coutumes des huitotos et des correguajes de Colombie. Bull. Soc. Américc. Belg. (Dec. 1931) 39.

10. Claes, Florent. Chez les huitotos et correguajes. Bull. Soc. Roy. Belg. Geogr. 56 (1932) 25–51.

11. Clinquart, E. Contribution à l'étude de la liane yajé et de son alkaloide. Journ. Pharm. Belg. 8 (1926) 671.

12. Cooper, John M. Stimulants and narcotics. *in Handbook of South American Indians*. [Ed. J. H. Steward] Smithson. Inst. Bur. Am. Ethnol. Bull. 143 (1949) 552, map 14.

13. Costa, Oswaldo de Al. and Luis Faria. A planta que faz sonhar. Rev. Fl. Med. 2: no. 10 (1936).

14. Costa, Oswaldo de Al. and Luis Faria. Rev. Assoc. Brasil. Farm. 17 (1936) 265.

15. Crévaux, J. Voyages dan l'Amérique du Sud. (1883) 362, 536.

16. Elger, F. Helv. Chim. Act. 11 (1928) 162.

17. de Calella, Plácido. Apuntes sobre los indios Sionas del Putumayo. Anthropos 35–36 (1944) 749.

18. de Szyszlo, Vitold. La naturaleza en la América ecuatorial. (1955) 250.

19. Ducke, Adolfo. O cabi do Pará. Arqu. Serv. Forest. 2 (1943) 13.

20. Ducke, Adolfo. Plantas de cultura pre-colombiana na Amazônia brasileira. Notas sobre as especies ou formas espontâneas que supostamente lhes teriam dado origem. Bol. Técn. Instit. Agron. Norte, no. 8 (1946) 5.

21. Fabre, René. Quelques plantes médicinales de l'Amérique Latine: leur utilisation thérapeutique. Rev. Gen. Sci. Pures Appl. 62 (1955) 49.

22. Fischer Cardenas, G. Estudio sobre el principio activo del *yagé*. [Unpublished thesis, Univ. Nac., Bogotá.] (1923).

23. Fosberg, F. R. Principal economic plants of tropical America. *in Plants and Plant Sciences in Latin America.* [Ed. F. Verdoorn] (1945) 28.

24. Gagnepain, F. Observations sur le yajé. Rev. Bot. Appl. Colon. 10 (1930) 293.

25. García-Barriga, Hernando. Conferencias de botánica médica [Mimeographed] (1950) 103, 151–152.

26. Hammerman, A. F. Bull. Appl. Bot. Gen. Pl. Breed. (1929) 165.

27. Hammerman, A. F. Le yagé en Amazonie. Rev. Bot. Appl. Agric. Colon. 10 (1930) 600.

28. Hardenberg, W. E. The Putumayo, the devil's paradise. (1913) 86.

29. Hartwich, C. Die menschlichen Genussmittel. (1911).

30. Henry, Thomas Anderson. The plant alkaloids. Ed. 4 (1949) 488.

31. Herrera, Fortunato L. Sinopsis de la flora de Cuzco. 1 (1941) 288.

32. Hesse, Erich. Narcotics and drug addiction. (1946) 112.

33. Hill, Albert F. Economic botany. Ed. 1 (1937) 294; ed. 2 (1952) 283, 511, t. 143.

34. Hoehne, F. Plantas e substancias vegetais tóxicas e medicinais do Brasil. (1939) 171.

35. Karsten, Rafael. Beiträge zur Sittengeschichte der südamerikanischen Indianer. II. Berauschende und narkotische Getränke unter den Indianern Südamerikas. Act. Acad. Aboensis Hum. Abh. 1 (1920) 39.

36. Karsten, Rafael. The civilization of the South American Indians. (1926) 324 ff., 473.

37. Karsten, Rafael. The head-hunters of western Amazonas. (1935) 343–346, 432–451.

38. Keller, O. and Franz Gottauf. Über einigen in Heimatlande arzneilich benutzte bolivianische Drogen. Arch. Pharmaz. 267 (1929) 373.

39. Koch-Grünberg, Theodor. Zwei Jahre unter den Indianern. 1 (1909) 298.

40. Koch-Grünberg, Theodor. Vom Roraima zum Orinoco. 1 (1917) 324.

41. Le Cointe, Paul. A Amazonia brasileira III. Arvores e plantas uteis (1934) 70, 471.

42. Lewin, Louis. Sur une substance enivrante, la banisterine, extraite de *Banisteria Caapi*. Comptes Rend. Acad. Sci. 186 (1928) 469.

43. Lewin, Louis. Untersuchungen über *Banisteria Caapi* Spr. Arch. f. exp. Pathol. Pharmakol. 129 (1928) 133.

44. Lewin, Louis. Arch. f. exp. Pathol. Pharmakol. 129 (1928) 324.

45. Lewin, Louis. Gifte und Vergiftungen. Ed. 4 (1929) 687.

46. Lewin, Louis. Phantastica — narcotic and stimulating drugs. (1931) 140.

47. Macbride, Francis J. Flora of Peru. Field Mus. Nat. Hist. Publ. 288, Bot. Ser. 11 (1931) 34.

48. Macbride, Francis J. Flora of Peru. Field Mus. Nat. Hist. Publ. 653, Bot. Ser. 13 (1950) 821 ff.

49. MacCreagh, Gordon. White waters and black. (1926) 373–384.

50. Magelli, José M. Carta sobre las misiones dominicanas del Oriente. Carta sexta. La misión de Macas. (1890) 17.

51. Manske, R. H. and H. L. Holmes. The alkaloids — chemistry and physiology. 2 (1952) 393.

52. Maxwell, Mary Mitchell. Caapi, its source, use and possibilities. [Unpublished ms.] (1937).

53. McGovern, William Montgomery. Jungle paths and Inca ruins. (1927) 262.

54. Michiels, M. and E. Clinquart. Sur des réactions chimiques d' identification de la yagéine. Bull. Acad. Roy. Méd. Belg., s. 5, 6 (1926) 19.

55. Möller, Knud O. Rauschgifte und Genussmittel. (1951) 78.

56. Mors, Walter B. and Perola Zaltzman. Sôbre o alkalóide de *Banisteria Caapi* Spruce e do *Cabi paraensis* Ducke. Bol. Inst. Quim. Agric. no. 34 (1954) 17.

57. Morton, C. V. A new *Banisteria* from Brazil and British Guiana. Proc. Biol. Soc. Wash. 43 (1930) 157.

58. Morton, C. V. Notes on *yagé*, a drug plant of southeastern Colombia. Journ. Wash. Acad. Sci. 21 (1931) 485 ff.

59. Niedenzu, F. Über die Stammpflanzen des Yageins. Pharmaz. Zeit. 73 (1928) 141.

60. O'Connell, F. D. and E. V. Lynn. The alkaloids of *Banisteriopsis inebrians* Morton. Journ. Am. Pharm. Assoc. 42 (1953) 753.

61. Orton, James. The Andes and the Amazon. (1871) 171.

62. Pardal, Ramón. Las drogas estupefacientes e ilusiógenas del indio americano. Rev. Geogr. Amer. 3 (1936) 1.

63. Pardal, Ramón. Medecina aborigen americana. Humanior, Secc. C, 3 (1937) 273.

64. Penna, Meira. Diccionario brasileiro de plantas medicinais. Ed. 3 (1946) 55.

65. Pérez-Arbeláez, Enrique. Plantas útiles de Colombia. Ed. 1 (1935) 44; ed. 2 (1947) 326, 334; ed. 3 (1956) 460.

66. Perrot, E. and R. Hamet. Le yagé, plante sensorielle des indiens de la région amazonienne de l'Equateur et de la Colombie. Comptes Rend. Acad. Sci. 184 (1927) 1266.

67. Perrot, E. and R. Hamet. Yagé, ayahuasca, caapi et leur alcaloïde: télépathine ou yagéine. Trav. Lab. Mat. Méd. Pharm. Galén. 18: pt. 2 (1927) 1.

68. Pynaert, L. Florent Claes — botaniste belge, explorateur. Publ. Jard. d'Agrément, Bull. Mens. Doc. Bot. Hort. d'Hort. Prat. Régions temp. trop. (July 1937) 45.

69. Reinburg, P. Contribution à l'étude des boissons toxiques des indiens du Nord-ouest de l'Amazone, l'ayahuasca, le yajé, le

huanto. Journ. Soc. Américic. Paris, n.s., 13 (1921) 25–54, 197–216.

70. Reko, Victor A. Ayahuasca, der Trank der grauenhaften Träume. Heil-Gewurzpfl. 15: pt. 3 (1932–33) 135.

71. Reko, Victor A. Magische Gifte — Rausch- und Betäubungsmittel der Neuen Welt. (1936) 89.

72. Reutter [K.]. Du yagé ou aya huesca. Schweiz. Apotheker Zeit. 25 (1927) 289.

73. Rivet, Paul. Les indiens Colorados. Journ. Soc. Américic. Paris 2 (1905) 201.

74. Rivet, Paul. Contributions à étude des langues Colorado et Cayapa. Journ. Soc. Américic. Paris 4 (1907) 49.

75. Rivet, Paul. Les indiens Jivaro. L'Anthrop. 18 (1907) 592.

76. Robinson, C. B. *in* Small: *North American Flora* 25 (1910) 131.

77. Rocha, Joaquín. Memorandum de viaje (regiones amazónicas). El Mercurio (Bogotá) (1905) 43.

78. Rouhier A[lexandre]. Le *yagé:* plante télépathique. Paris medical, partie para médicale 52 (1924) 341.

79. Rouhier, A[lexandre]. Les plantes divinatoires. Rev. Métapsych. (1926) 325–331.

80. Rusby, H. H. South American exploration. Journ. Am. Pharm. Assoc. 12 (1923) 54.

81. Rusby, H. H. The aboriginal uses of caapi. Journ. Am. Pharm. Assoc. 12 (1923) 1123.

82. Rusby, H. H. The pharmacodynamics of caapi. Journ. Am. Pharm. Assoc. 13 (1924) 98.

83. Safford, W. E. Narcotic plants and stimulants of the ancient Americas. Ann. Rept. Smithson. Inst. 1916 (1917) 411–413.

84. Sandeman, Cristopher. Thyme and bergamot. (1947) 24.

85. Schery, Robert W. Plants for man. (1952) 288.

86. Schultes, Richard Evans. Plantae Austro-Americanae VIII. Bot. Mus. Leafl. Harvard Univ. 16 (1953) 90.

87. Schultes, Richard Evans. Plantae Austro-Americanae IX. Bot. Mus. Leafl. Harvard Univ. 16 (1954) 202, t. 30, bottom figure.

88. Seil, Harvey A. and Earl B. Putt. The chemical examinination of caapi. Journ. Am. Pharm. Assoc. 13 (1924) 99.

89. Simson, Alfred. Travels in the wilds of Ecuador. (1886) 196.

90. Spruce, Richard. Notes of a botanist on the Amazon and Andes. [Ed. A. R. Wallace] 2 (1908) 414–425.

91. Taylor, Norman. Flight from reality. (1949) 175.

92. Tyler, Charles D. The river Napo. Geogr. Journ. 3 (1894) 480.

93. Uribe Uribe, Lorenzo. Botánica. Ed. 3 (1948) 210.

94. Villarejo, Avencio. Así es la selva. (1943) 121.

95. Villavicencio, Manuel. Geografía de la República del Ecuador. (1858) 371.

96. von Hagen, Victor Wolfgang. Scarlet men. Nat. Hist. 40 (1937) 389.

97. von Hagen, Victor W[olfgang]. Realm of the Incas. (1957) 110.

98. von Martius, Carl F. P. Nomina plantarum in lingua tupi. Bull. K. Bayer. Acad. Wissensch. (1858) 1–6.

99. von Martius, Carl F.P. Zur Ethnographie Amerikas zumal Brasiliens. (1867) 388.

100. Whiffen, Thomas. The northwest Amazon. (1915) 139.

101. White, O. E. Botanical exploration in Bolivia. Brooklyn Bot. Gard. Rec. 11 (1922) 102.

102. Williams, Llewellyn. The death vine—ayahuasca. Field Mus. News 2, no. 8 (1931) 3.

103. Williams, Llewellyn. The woods of northeastern Peru. Field Mus. Nat. Hist. Publ. 377, Bot. Ser. 15 (1936) 257.

104. Wolfe, O. and K. Rumpf. Über die gewinnung von Harmin aus einer südamerikanischen Liane. Arch. Pharmaz. 266 (1928) 188.

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THE EFFECTS OF CERTAIN GENES ON THE OUTER PISTILLATE GLUME OF MAIZE

BY

WALTON C. GALINAT

A comparison of the effects which various genes have on the structure of a given plant-organ should sometimes reveal which of the loci concerned were involved in the previous evolution of that organ and which of them might, during domestication of the species, contribute to its further evolution. The extreme susceptibility of the outer pistillate glume[1] in the maize tribe (*Maydeae*) and the related tribe *Andropogoneae* to evolutionary modifications suggests that the genetic variation affecting development of this organ in maize (*Zea Mays* L) may reflect some of its evolutionary changes. The changes in glume structure were drastic during evolution leading to the formation of the cupulate fruit case (Galinat, 1956). This organ evolved from a long foliaceous bract (*Erianthus* spp.) to a shorter, coriaceous structure marked by various types of sculpturing (*Manisuris* spp. ; *Hackelochloa* spp.) and, finally, to a highly lignified glume which is specialized in shape, texture and plane of divergence so as to bring about a closure of the narrow opening of a cupulate rachis-segment (*Euchlaena* and *Tripsacum*).

[1] Further mention of the glumes of maize will refer only to the outer pistillate ones.

Thus, we might expect that a study of the various glume phenotypes of modern maize would be revealing as to the past and possible further evolution of this glume during domestication.

Three dominant or semi-dominant genes which affect principally the outer pistillate glume were included in this study. They are as follows: (1) Papyrescent (*Pn* gene on chromosome-7); (2) Tunicate (*Tu* gene on chromosome-4); (3) Vestigial glume (*Vg* gene on chromosome-1). These genes were studied in heterozygous condition after they had been incorporated, by repeated backcrossing, into an isogenic background of a sweet corn (maize) inbred (Purdue 39). Their effects on the histological structure of this glume were examined in material prepared in the following manner: Normal (typical) and variant specimens were fixed at 18 days after pollination. This material was later embedded in paraffin, according to the usual procedure, and then cut in cross-section at 12 μ. The sections were then stained by the standard safranin-fast-green technique. Finally, a projection apparatus was used in making tracings from comparable slides.

Normal glumes. The glumes and other floral bracts of modern maize are so reduced that the mature grain emerges naked above them. Protection for the grain, which is provided by long floral bracts in most other grasses, is supplied by husks (modified leaf-sheaths) borne below the pistillate inflorescence (ear) on a condensed branch (shank).

The normal glume has papery lateral wings (Plate IX, fig. 3) and the entire structure is homologous to a leaf-sheath with sheath-auricles. The glume-sheath, which is the counterpart of the leaf-sheath, may be coriaceous in texture (in many South American varieties) or, more commonly, it may resemble its counterpart in teosinte

in being corneous or indurate (in teosinte-contaminated varieties from North and Central America). The degree of this induration has been used as an estimate of teosinte-introgression in archaeological maize, after the reliability of the method has been established (Galinat *et al*, 1956).

Internally, the mesophyll of the glume is divided into definite specialized regions. The induration is confined to a region of smaller cells extending from the outer epidermis to a line delimited by a row of vascular bundles about midway through a cross section (Plate X, fig. 3). As indicated by strong safranin staining, these smaller indurated cells are characterized by an accumulation of lignin in the secondary walls. The remainder of the glume, extending to the inner epidermis, consists of large parenchyma-cells. During final maturation of the glume, this parenchymatous tissue collapses from desiccation. The resulting shrinkage of the parenchyma toward the bundles causes an outline of the vascular system to be revealed as parallel ridges along the inner epidermis.

The vascular arrangement of the normal glume differs slightly from that which occurs in a vegetative leaf-sheath. The glume has smaller bundles and, since this organ is determinative, they converge at the apex. In the leaf-sheath these principal bundles remain parallel as they continue on into the blade. As in the leaf-sheath, the parallel bundles are of two sizes with the larger ones alternating with one or two smaller ones. The small cross connections which anastomose between the parallel bundles are confined to the apical region of the glume as compared to a distribution along the entire length of both the blade and sheath of the leaf. The glume wings are non-vascular as are the ligules and sheath-auricles of the leaf-sheath. It seems that these vascular differences between glumes and leaf-sheaths are more in the nature of minor modifications.

EXPLANATION OF THE ILLUSTRATION

PLATE IX. The outer pistillate glume of maize, as effected by various genes. Left and right specimens show dorsal and ventral views. 1, papyrescent (*Pn*); 2, tunicate (*Tu*); 3, normal; 4, vestigial glume (*Vg*). Twice natural size.

Photograph by FRANK WHITE

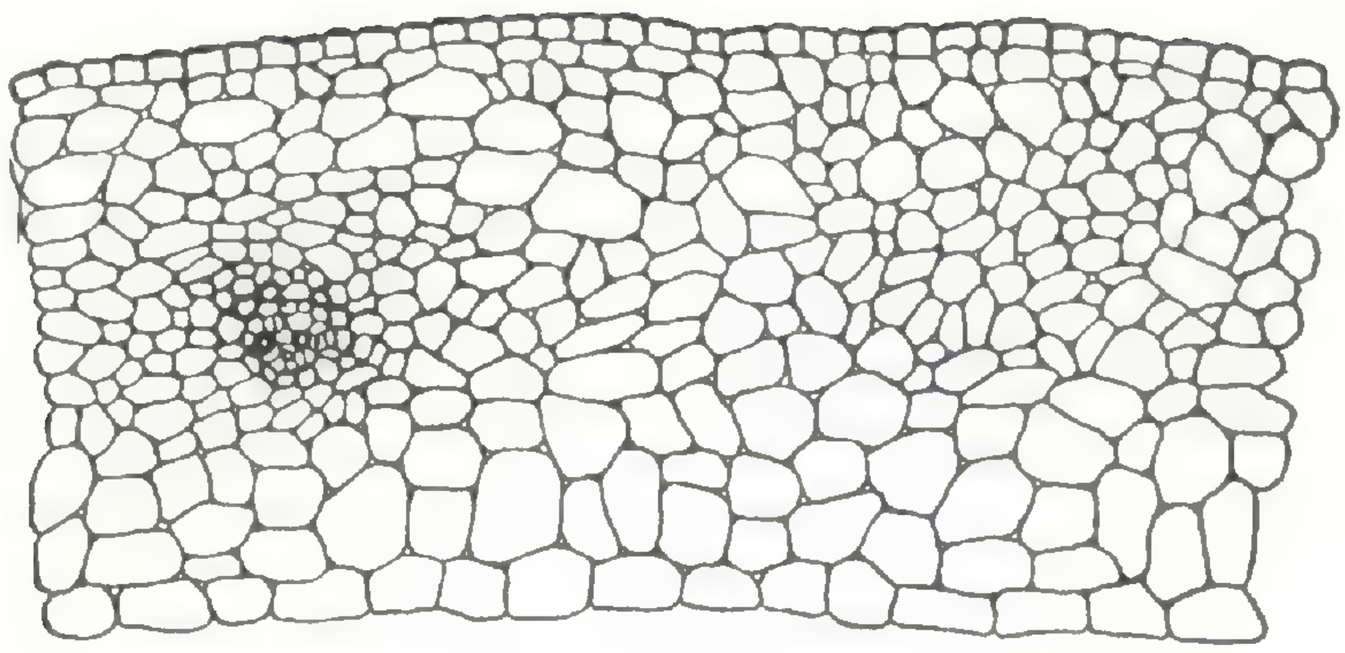
Plate IX

EXPLANATION OF THE ILLUSTRATION

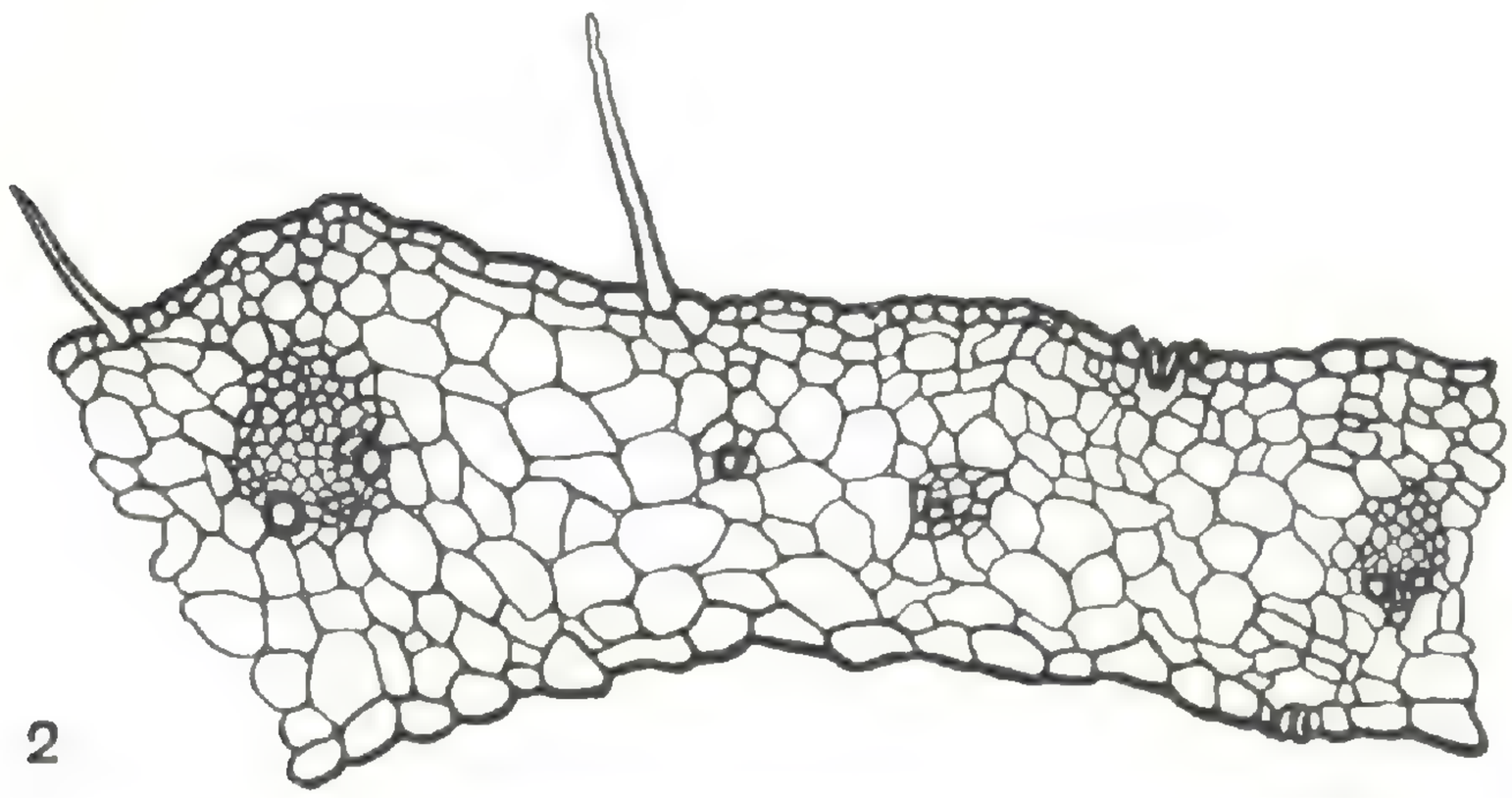
PLATE X. Projection tracings of comparable cross-sectional views of the outer pistillate glume as this organ is affected by certain genes. In each figure the outer (abaxial) epidermis is uppermost. 1, papyrescent (*Pn*); 2, tunicate (*Tu*); 3, normal; 4, vestigial glume (*Vg*). About 80 times natural size.

Drawn by WALTON C. GALINAT

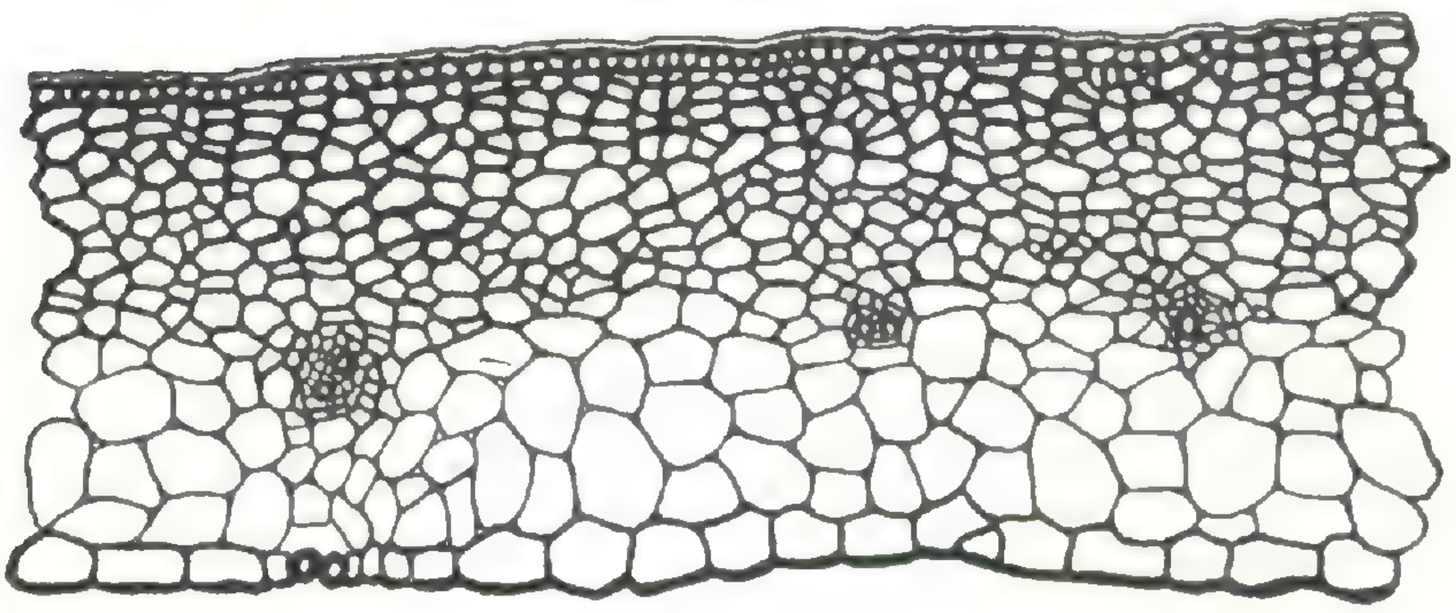
Plate X



1



2



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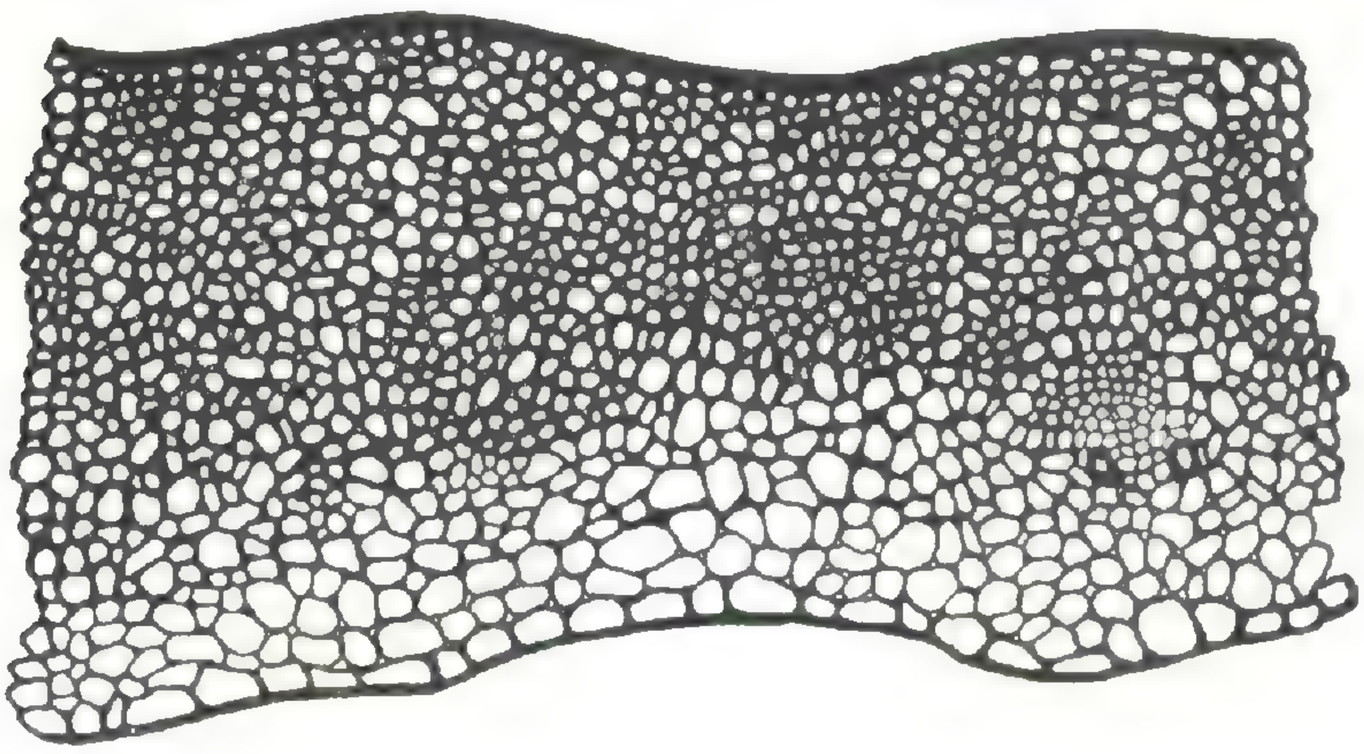


4

As in the leaf, stomata occur along both epidermal surfaces. In the glume, however, they are vestigial and obscure along the outer epidermis. Such reduction may result from the extreme lignification of the underlying tissue. Rather well-developed stomata are found on the inner surface directly opposite the larger vascular bundles. The fact that the maize-glume has stomata and yet does not have an opportunity to function in photosynthesis, seems to emphasize the leaf-like nature of this organ.

The outer epidermis has a glabrous cuticle and may acquire a brown, red or purple coloration from the action of certain genes. Epidermal pubescence is greatly reduced, except in the lateral wings.

Papyrescent glumes. This dominant mutant is characterized by glumes which upon final maturation become papery and similar in texture to that which occurs in lemmas, paleas and lateral wings of normal glumes, as well as in the ligules of normal leaves (Plate IX, fig. 1). These papyrescent glumes are usually slightly longer than the mature grain. A condition which is superficially similar to the papyrescent character develops in normal ears which are poorly matured. This simulation results from the protrusion of the lemmas, paleas and papery wings from normal glumes above chaffy or small grains.

The papyrescent character is likewise similar or identical with the "palee sviluppate" of Bonvicini (1932) and apparently with the recessive "semivestidos" of Andrés (1950). Our character for papyrescent glumes may have been incorrectly identified by Andrés as a recessive factor since the effects of this semi-dominant gene are not always readily apparent in the heterozygote. It has also been confused by Weatherwax (1954) with half-tunicate, from which, as will be pointed out later, it is histologically distinct. Furthermore, we find a counterpart of the

papyrescent condition in *Sorghum*, where it once led to the describing of a new species (*Sorghum papyrascens* Stapf), an error later corrected by Rangaswami and Panduranga (1936) who correctly identified it as a single gene mutant characterized by defective glume development. Papery glumes have also appeared in two X-ray induced mutants (*seminudoides* and *subnudoides*) of barley (Scholz, 1956). In these two recessive mutants, the floral bracts fragmentize away from the grain during threshing. Ordinarily the floral bracts of barley remain about the grain following threshing, except in the mutant named *nudoides*. The differences in the terminology of Sholz and Andrés, as applied to their particular mutants, refer to differences in the normal condition of the glumes in barley and maize. The term "seminudoides" (half-nude) applies to the barley mutant because normally the threshed barley grain is completely covered, while "semivestidos" (half-clothed) is better for the maize mutant because normally the maize grain is exposed.

Papyrescent glumes in maize consist largely of non-specialized parenchyma-cells which, at 18 days from pollination, are large and fleshy, being swollen with water (Plate X, fig. 1). During final maturation of the ear, dessication causes these parenchymatous glumes to shrink to a thin, almost transparent condition with the vascular bundles becoming prominent ridges (Plate IX, fig. 1). There is little contraction in length and width, however, and the glumes remain partially covering the surface of the mature grain. Finally, they become papery and brittle and are distinctly different from those glumes which protect the caryopses of other grasses.

The epidermal layers of the papyrescent glume approach those of the normal glume in regard to cell size, but differ from normal in being less lignified and in lacking stomata. Pubescence is usually confined to the mar-

ginal part of the glume. The vascular bundles are essentially normal in structure, although they are not so closely spaced.

The succulent nature of immature papyrescent glumes often encourages the destructive activities of ear-rotting fungi. This suggests that a hardening of these glumes, such as is caused by teosinte introgression, may promote resistance to pathogenic fungi.

The gene which produces this defective character has been previously designated as pseudopod (*Pp*) (Galinat and Mangelsdorf, 1955), but it now seems more desirable to change its name and symbol to papyrescent (*Pn*) (Galinat and Mangelsdorf, 1957). This change will call attention to its final papery character and its similarity to the "papyrascens" character of *Sorghum*, and will avoid confusion with the symbols for heterozygous pericarp color (*Pp*) as well. Our *Pn* gene was originally isolated from a Peruvian variety of maize (Mangelsdorf, 1948). It is located close to the *bd* (branched-silkless) gene near the end of the long arm of chromosome-7. Its linkage relations will be discussed in more detail in a future paper.

Tunicate glumes. The highest tunicate allele (*Tu*) from the series of multiple-alleles at the *Tu-tu* locus was chosen in order to study, in accentuated form, the effects of genes at this locus. Weaker alleles at the tunicate locus have intermediate effects on the length, shape and texture of the glume (Mangelsdorf, 1948). Further discussion of tunicate glumes will refer to the phenotype of the strongest tunicate allele (Plate IX, fig. 2).

The glumes of tunicate maize are like those of most other grasses in being long enough to enclose the grain and in being foliaceous. They differ therefore, in length and texture from the pistillate glumes characteristic of the American *Maydeae*, including normal maize, and of

Manisuris spp. in the *Andropogoneae*. In the evolutionary sequence leading to formation of the cupulate fruit case, tunicate glumes of maize are similar to the glumes of *Elyonurus tripsacoides* (Galinat, 1956).

Anatomically, tunicate glumes have all of the characteristics of a typical leaf-sheath, but on a reduced scale (Plate X, fig. 2). The close similarities of these organs may be enumerated as follows: (1) The inner (adaxial) and outer (abaxial) surfaces of tunicate glumes and leaf-sheaths are about equally pubescent with soft trichomes. This condition differs from that of the leaf-blade where pubescence is located chiefly on the upper (adaxial) epidermis and from that of the normal glume where the trichomes are confined to the lateral wings. (2) Both tunicate glumes and leaves (including sheath and blade) are herbaceous in texture because their mesophyll lacks the region of lignified cells which characterizes the normal glume. (3) Stomatal development in tunicate glumes resembles that of the leaf-sheath and differs from the condition found in the normal glume. Tunicate glumes and leaf-sheaths have well-developed stomata on both surfaces although they are more frequent and functional on the outer epidermis. As noted previously, if well-developed stomata occur in the normal glume, they are located on the inner surface. (4) The vascular system of tunicate glumes is more similar to the venation of leaves than it is to that of normal glumes. In both tunicate glumes and leaves, the anastomosing venation connects the principle bundles at irregular intervals along their entire length rather than just in the distal region as in the normal glume. (5) The structure of tunicate bundles is frequently identical to that of leaf bundles in contrast to the more reduced veins of normal glumes (Plate X, figs. 2 and 3). All of these anatomical comparisons support the contention that the tunicate locus controls evo-

lution from the primitive foliaceous state which is typical of glumes in general to the highly specialized glumes of modern maize.

Vestigial glumes. The vestigial glume (*Vg*) mutant reported by Sprague (1939) is of particular morphological and agronomic significance. Originally this naked-flowered character was thought to be of no economic value because it was associated with pollen-blasting tassels. The discovery of modifying genes which usually permit abundant pollen production in *Vg* tassels, aroused interest in the utilization of the *Vg* character to improve the structure of the sweet corn (maize) ear (Galinat, 1951, 1953). It became apparent, however, that in order to insure pollen-production in inbred lines grown under various environmental conditions, it would be necessary to have tassels with glumes of normal length on *Vg* plants bearing glumeless ears. This desired *Vg* phenotype became a reality after a certain weak tunicate allele derived from the race "Chapalote" was combined with the *Vg* gene (Galinat, 1955, 1957). As a result, the agronomic development and testing of sweet corn hybrids with this new *Vg* phenotype is now in progress.

Vg glumes deviate from normal in the opposite direction from the deviation of tunicate glumes (Plates IX and X, figs. 2, 3, 4). In comparison to normal ones, *Vg* glumes are thicker, shorter and have increased lignification, while *Tu* glumes are thinner, longer and have reduced lignification (lacking the lignified region in the mesophyll). The progressive thickening of glumes in this series of three types (*Tu;* normal; *Vg*) appears to result largely from the development and proliferation of many small lignified cells in a region just under the abaxial epidermis. The smaller the cell in this region, the thicker the deposit of lignin in the secondary wall (Plate XI).

The accumulation of this lignin is known to be secondary, in that it occurs after the glumes have already attained optimum length and during the development of the caryopsis. If fertilization does not occur, then the glumes remain non-lignified and finally become papery. If only a portion of the ear is fertilized, then only those glumes which are either directly associated with fertilized ovaries or indirectly associated by being adjacent to spikelets with fertilized ovaries will become lignified. This immediate effect of fertilization in stimulating lignification of maternal tissue occurs also in teosinte and *Tripsacum*. Also the cupule of maize, as well as its counterpart in these close relatives, is included in the same metaxenial phenomenon.

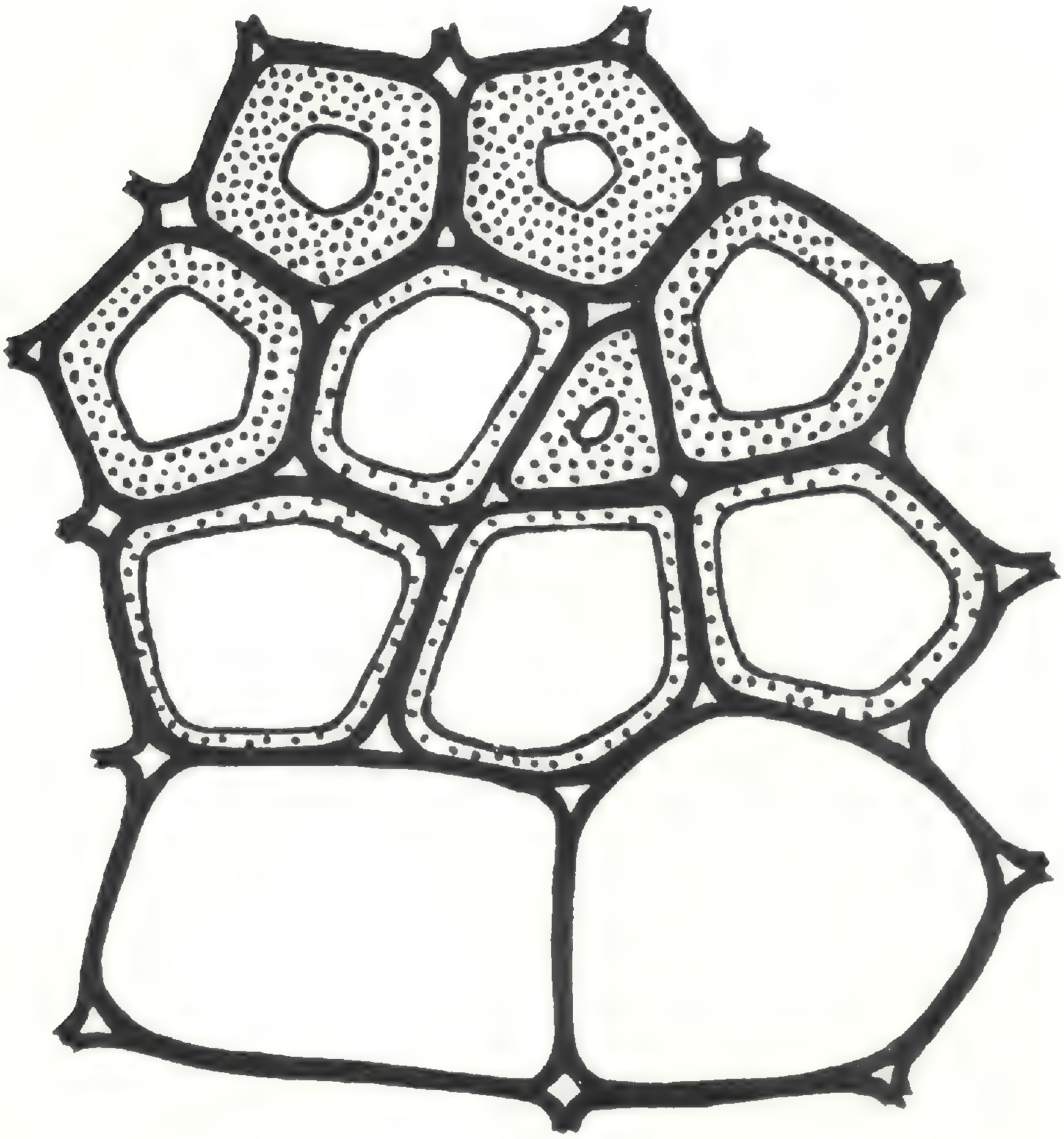
Certain features of the vestigial glume syndrome seem to be correlated with morphological homologies. The effect of the *Vg* gene in reducing glume size appears to be accomplished largely by suppression of the lateral wings (probably sheath-auricles), with the remaining portion representing a small, highly lignified sheath (compare figs. 3 and 4 in Plate IX). In addition to the lateral wings of the glumes, the *Vg* gene also causes, under certain conditions, a reduction of the lateral wings of the cupules and the ligules of the leaves; this last-named effect was noted first by Laughman (1956). Glume wings and ligules have at least two features in common in that both of them are papyraceous in texture and are situated as erect prolongations of the sheath, or its homologue, adjacent to the actual or theoretical insertion-point of the blade. Furthermore, these structures appear to be homologous, as is suggested by the vegetative leaves of certain grasses (*Ammophila arundinacea*) with blades that are narrower than their sheaths. In such grasses, the lateral portions of the "ligule" elongate and develop as sheath-auricles with the same textural characters as the

EXPLANATION OF THE ILLUSTRATION

PLATE XI. A few contrasting cell types from a cross-sectional view of the outer pistillate glume of an ear with the vestigial glume character. Note that the smaller cells have a higher degree of lignification in the secondary walls (the stippled area). About 500 times natural size.

Drawn by WALTON C. GALINAT

Plate XI



sheath, whereas the portion which is adjacent to the blade is reduced and papery. A similar phenomenon occurs in the lemmas of many grasses (*Avena* and *Bromus*) where the blade is modified into a narrow awn.

The effect of the *Vg* gene in reducing the size of the cupule wings is not necessarily comparable to its effects on either glume wings or ligules. Rather the small size of *Vg* spikelets may decrease their capacity to depress the adjacent rachis-internode during youth and thereby result in shallow cupules.

Discussion

The features of *Tu* and *Vg* glumes differ from normal in opposite ways and in doing so they reflect glume-types involved in the early evolution of maize and *Tripsacum* in the American *Maydeae*. Teosinte is thought to have developed later from the hybridization of maize and *Tripsacum* (Mangelsdorf and Reeves, 1939). The foliaceous character of tunicate glumes is typical of the Andropogonaceous grasses (as in *Elyonurus tripsacoides*). Also it is a starting point from which the glumes of maize, *Tripsacum*, and possibly *Manisuris* could have evolved (Galinat, 1956). In the differentiation of *Tripsacum* and *Manisuris*, the glumes underwent reduction and lignification or sculpturing while the paired grain-bearing spikelets were reduced to singleness. Maize evolved in a separate direction which was controlled largely by mutation at the *Tu-tu* locus (Mangelsdorf, 1948). Nevertheless, a latent ability to evolve a Tripsacoid-type of outer glume might have been retained in modern maize and finally expressed as the *Vg* mutant. We conclude that in regard to this series (*Tu*; normal; *Vg*), the structure of tunicate glumes indicates that the *Tu-tu* locus may have been involved in previous evolution of the maize glume and that the mutation to the

vestigial glume condition demonstrates a potential in maize to evolve a Tripsacoid-type of glume.

The evolutionary changes resulting in shorter glumes during the domestication of maize could hardly have involved mutation at the *Vg–vg* locus. The *Vg* gene is a rare type of dominant mutation which seems to be of recent origin. Furthermore, it is not known to be part of a multiple-allelic series such as has been reported for the *Tu-tu* locus. There is also strong morphological evidence that the *Vg* gene has not been active in maize evolution. If such *Vg* activity had occurred, then it would be revealed by a characteristic reduction of the lateral wings of glumes. On the contrary, these wings are well-developed and papery in both modern and archaeological maize. In teosinte and *Tripsacum*, however, the glume wings are somewhat reduced and highly lignified.

In the series *Tu;* normal; *Vg*, decreases in glume-length are accompanied by increases in the thickness of the outer lignified zone. Since lignification of this outer zone of the glume occurs at the same time as kernel-development, there may be competition for the available energy. In the tunicate series of alleles (Mangelsdorf and Mangelsdorf, 1957) some of the energy conserved from shorter glumes is apparently diverted to increased grain production in spite of an increase in glume-lignification. Experiments are now in progress to determine the effect of the *Vg* gene on yield of mature grain.

Pn glumes exemplify a condition which does not fit into this pattern of variation and, notwithstanding the suggestion of Andrés (1950), could scarcely have exercised a protective role at any stage in the evolution of maize. The only possible evolutionary counterpart of papyrescent glumes in other grasses appears to be represented by a certain degenerate change found in several

varieties of *Sorghum* (Rangaswami and Panduranga, 1936). A papery condition which is apparently similar to that of papyrescent maize has been produced by two X-ray induced mutations in barley (Scholz, 1956).

Acknowledgments

During the preparation of the manuscript, many helpful suggestions were made by Professor P. C. Mangelsdorf of Harvard University. Professor Angelo Bianchi of Pavia University helped in the preparation of some of the slides.

LITERATURE CITED

Andrés, J. M., 1950. Granos semivestidos, restos de un charácter ancestral del maíz. Rev. Argentina Agron. 17: 252–256.

Bonvicini, M., 1932. Sulla ereditarietà di una anomalia del maiz. L'Italia Agricola 69: 3–9.

Galinat, W. C., 1951. Glumeless hybrid sweet corn. Jour. Hered. 42: 114–116.

——, 1953. Resistance to blasting of *Vg* tassels. Maize Gen. Coop. News Letter 27: 76.

——, 1955. Maize with vestigial-glume ears and normal tassels. Maize Gen. Coop. News Letter 29: 27.

——, 1956. Evolution leading to the formation of the cupulate fruit case in the American *Maydeae*. Bot. Mus. Leafl. Harvard Univ. 17: 217–239.

——, 1957. The effect of weak tunicate alleles on the expression of the *Vg* gene. Maize Gen. Coop. News Letter 31: 68.

Galinat, W. C., and P. C. Mangelsdorf, 1955. Pseudopod, a possible allele of vestigial glume. Maize Gen. Coop. News Letter 29: 26.

——, 1957. Papyrescent maize. Maize Gen. Coop. News Letter 31: 67.

Galinat, W. C., P. C. Mangelsdorf, and L. Pierson, 1956. Estimates of teosinte introgression in archaeological maize. Bot. Mus. Leafl. Harvard Univ. 17: 101–124.

Laughnan, J. R., 1956. Effect of *Vg* on development of the ligule. Maize Gen. Coop. News Letter 30: 67.

Mangelsdorf, P. C., 1948. The role of pod corn in the origin and evolution of maize. Ann. Mo. Bot. Gard. 35: 377–398.

—— and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exper. Sta. Bull. 574.

Mangelsdorf, P. C., and H. P. Mangelsdorf, 1957. Genotypes involving the *Tu-tu* locus compared in isogenic stocks. Maize Gen. Coop. News Letter 31: 65–67.

Rangaswami Ayyanger, G. N., and V. Panduranga Rao, 1936. *Sorghum papyrascens* Stapf. Jour. Indian Bot. Soc. 15: 139–142.

Scholz, F., 1956. Mutationsversuche an Kulturpflanzen V. Die Vererbung zweier sich variabel manifestierender Ubergangmerkmale von bespelzter zu nackter Gerste bie röntgeninduzierten Mutanten. Die Kulturpflanze 4: 228–246.

Sprague, G. F., 1939. Heritable characters in maize 50—Vestigial Glume. Jour. Hered. 30: 143–145.

Weatherwax, P., 1954. Indian corn in old America. The Macmillan Co., New York, 253 pp.

BOTANICAL MUSEUM LEAFLETS
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ORCHIDACEAE NEOTROPICALES IV
NOTES ON THE GENUS *Caularthron* RAF.

BY

RICHARD EVANS SCHULTES

CAULARTHRON was recognized by Rafinesque as a generic concept distinct from *Epidendrum* as early as 1836. It was treated as a special section of *Epidendrum* by Lindley in 1841 under the name *Diacrium*. Section *Diacrium* was raised to generic status by Bentham in 1881. This is the name which has been applied to the genus by most subsequent orchidologists.

Were the genus large or had it become important in horticulture, the resumption of an earlier and unfamiliar name might be unfortunate; and the best procedure might be an attempt to include *Diacrium* amongst the officially conserved generic names. I believe that this procedure should be reserved for names of large genera of great economic or horticultural importance, where the abandonment of a long and well established epithet would lead to extreme confusion. Therefore, I recommend the substitution of *Caularthron* for *Diacrium*.

Our herbaria have not had abundant material of *Caularthron*, nor does the genus appear to have become a wide favorite in horticulture. In great part owing to these circumstances, it has not been so thoroughly understood as we might wish. Recent collections of *Caularthron* in Middle America, northern South America and Trinidad

and Tobago have added somewhat to our knowledge of the range and variability of the genus, but there still remains much to clarify.

In preparing the orchid section for the *Flora of Trinidad and Tobago*, I have had to consider critically the concepts which have been known as *Diacrium bicornutum* and *Diacrium indivisum*. A study of the available herbarium specimens and of the very superior material preserved in alcohol and sent in recently by Dr. Wilbur G. Downs and Dr. T. H. G. Aitken of Port-of-Spain, Trinidad, made it early apparent that the fundamental problems involved could not satisfactorily be handled without an examination of the generic concept as a whole. The present paper embodies the results of that examination.

I wish to thank the officials of the following herbaria for making available material entrusted to their care: Reichenbach Herbarium (in the Naturhistorisches Museum in Vienna); Gray Herbarium; Royal Botanic Gardens at Kew; New York Botanical Garden; United States National Herbarium; Chicago Natural History Museum and Missouri Botanical Garden. Material from these herbaria has supplemented the large collection of *Caularthron* preserved in the Orchid Herbarium of Oakes Ames of the Botanical Museum of Harvard University. It is, furthermore, a pleasure for me to thank Mr. G. C. K. Dunsterville for kind permission to reproduce two carefully executed drawings prepared for his forthcoming book of illustrations of Venezuelan orchids.

When Bentham described *Epidendrum bicornutum* in 1834 on the basis of material from Trinidad, he stated that he had consulted Lindley concerning its generic status, and had received the opinion that it "is certainly a new species; but I think it cannot be separated from *Epidendrum*. The only distinction between it and that Genus consists in the labellum being distinct from the

column: but you will find various degrees of separation between those parts . . .'' in several species ''. . . which nobody can doubt are genuine *Epidendra* . . . Should you, however, be of opinion that it nevertheless must form a new Genus, its character will have to depend upon the large size of the *petals* and the slight adhesion of the sepals at their base.'' Seven years later, Lindley erected his subgeneric concept *Diacrium* on the basis of *Epidendrum bicornutum*. Then, in 1881, when he raised *Diacrium* to generic status, Bentham wrote that ''the peculiar bicornute labellum, neither adnate to nor parallel with the column, gives the flower a very different aspect from that of true species of *Epidendrum* and can not be included in them without doing violence to the generic character.''

Having now at hand material from a wide geographic range—all with certain diagnostic characters which show no variation—I believe that the best interests of orchid classification may be served by keeping the concept distinct on a generic level. It is obviously very closely allied to *Epidendrum*, and some of the differences used to separate it may appear to be superficial. Nevertheless, it would seem that they represent perhaps a definite tangential evolutionary trend which ought to be recognized.

There can be no doubt that *Caularthron* should be used as the name for this generic concept in preference to *Diacrium*. There is a widespread aversion to the acceptance of many names proposed by Rafinesque. But I am sure that most botanists will agree with Merrill (Merrill, E.D.: ''Index Rafinesquianus'' (1949) 26, 29) that ''. . . where a new Rafinesque name was based wholly on a previously described or illustrated species of some other author, all we have to do to understand the application of the Rafinesque name is to determine the status of the originally described form . . . Thus it seems to be a logi-

cal course to follow to continue to select the few sound grains from the overwhelming amount of chaff in the Rafinesque technical botanical papers, even if, occasionally, some more or less universally used generic or specific name might fall before those proposed by Rafinesque at earlier dates."

No greater precision could be desired than that which we find in Rafinesque's description of *Caularthron* as a new genus. He not only published a very adequate description which makes definite references to key morphological characters separating the concept from *Epidendrum*, but, in a day when few botanists even mentioned what we now call types, he named the concept on which he was basing *Caularthron* by citing Hooker's *Epidendrum bicornutum* and referring to its place of publication. The later name for this same generic concept, *Diacrium*, was likewise based on *Epidendrum bicornutum*. The fact that, in second place under his generic description, Rafinesque made the new name *Caularthron umbellatum*, citing as basis for it *Epidendrum stenopetalum* Hook., does not militate against the wisdom or the necessity of accepting as valid his generic name, especially so since his generic description is obviously based on *Epidendrum bicornutum* and not on the very distinct *E. stenopetalum*.

Caularthron *Rafinesque* Fl. Tellur. 2 (1836 [1837]) 40, *pro parte*.

Epidendrum Linnaeus sect. *Diacrium* Lindley in Hooker Journ. Bot. 3 (1841) 81; Bot. Reg. 31 (1845) Misc. 23; Fol. Orch. (1853) Epidendrum 3; Reichenbach fil. in Walpers Ann. Bot. 6 (1862) 345.

Diacrium (Lindl.) Bentham in Journ. Linn. Soc. 18 (1881) 312; Bentham & Hooker fil. Gen. Plant. 3 (1883) 526; Hemsley Biol. Centr.-Am. Bot. 3 (1883) 221; Warner & Williams, Orch. Alb. 4 (1885) t. 157;

Rolfe in Gard. Chron. 2, ser. 3 (1887) 44; Pfitzer in Engler & Prantl Nat. Pflanzenfam. II, 6 (1888) 146; Veitch, Man. Orch. Plant. 6 (1890) 78; L'Orchidoph. (1891) 378; Rolfe in Lindenia 7 (1891) 19; Cogniaux in Martius Fl. Bras. 3, pt. 5 (1901) 186; Stein, Orchideenb. (1892) 214; Bois, Les Orch. (1893) 74; Kerchove, Livre des Orch. (1894) 264; Linden, Orch. Exot. (1894) 751; Cogniaux in Urban Symb. Antill. 6 (1910) 538; Schlechter, Die Orchideen (1915) 214; Ames ex Standley in Field Mus. Nat. Hist. Publ. 391 (1937) 210; L. O. Williams in Ann. Mo. Bot. Gard. 33 (1946) 378; Hoehne, Icon. Orch. Bras. (1949) 208; P. H. Allen in Orch. Journ. 2 (1953) 185; Ames & Correll in Fieldiana: Bot. 26 (1953) 405; Foldats in An. Univ. Centr. Venez. 34 (1953) 276.

Caularthron may be distinguished from *Epidendrum* on the basis of the characters set forth in the following key.

A. Labellum vulgo ad columnam variabiliter adnatum et cum ea parallelum, supra numquam protuberantibus elevatis subtus excavatis ornatum. ——*Epidendrum*

Aa. Labellum a columna liberum, a columnae basi angulatim patens, supra protuberantibus duabus elevatis subtus excavatis ornatum *Caularthron*

Epiphytic or semi-epiphytic herbs with fleshy pseudobulbose, solid or frequently insect-hollowed stems. Leaves few, borne at apex of pseudobulbs, rigidly subcarnose-coriaceous. Inflorescence terminal, simple, racemose. Flowers few to numerous, showy, short-pedicellate. Sepals free, spreading, subequal. Petals rather similar to sepals. Lip free and spreading from base of column, 3-lobed; lateral lobes conspicuously tooth-like; mid-lobe triangular or triangular-lanceolate; disk raised between lateral lobes into 2 hollow, often horn-like calluses opening from below to form 2 conspicuous inden-

EXPLANATION OF THE ILLUSTRATION

PLATE XII. CAULARTHRON BICORNUTUM (*Hook.*) *Rafinesque.* Grown in the greenhouse of F. W. Hunnewell, Wellesley, Massachusetts.

Photograph by Ross W. BAKER
Courtesy of American Orchid Society, Inc.

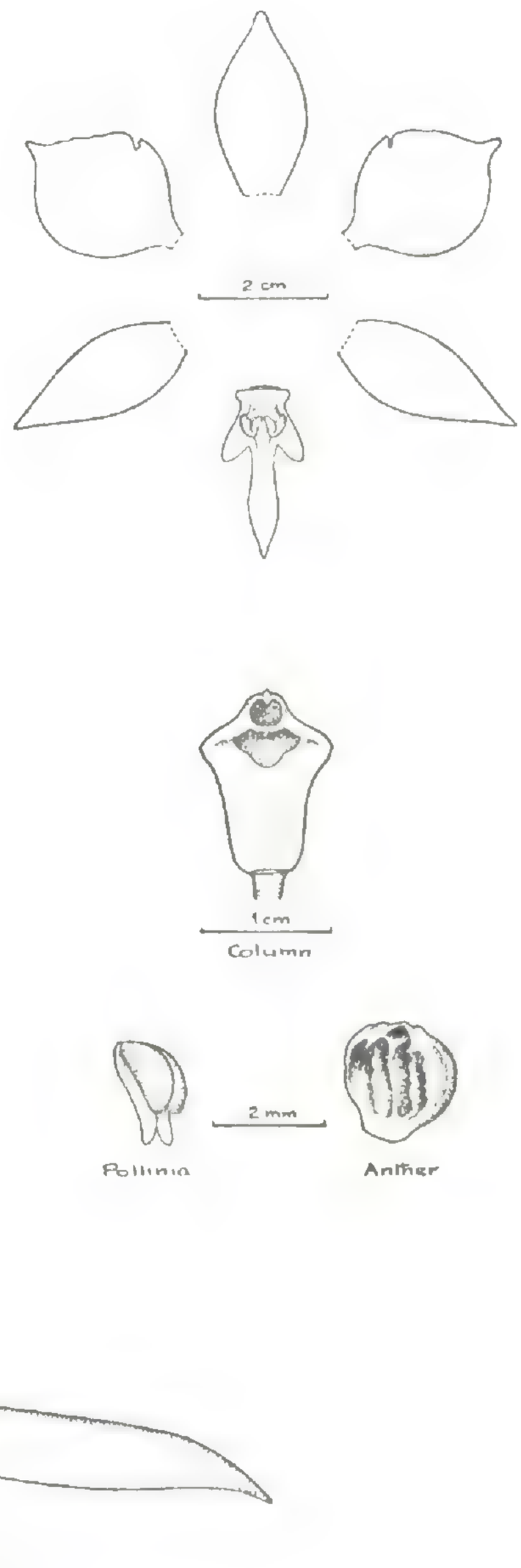
Plate XII

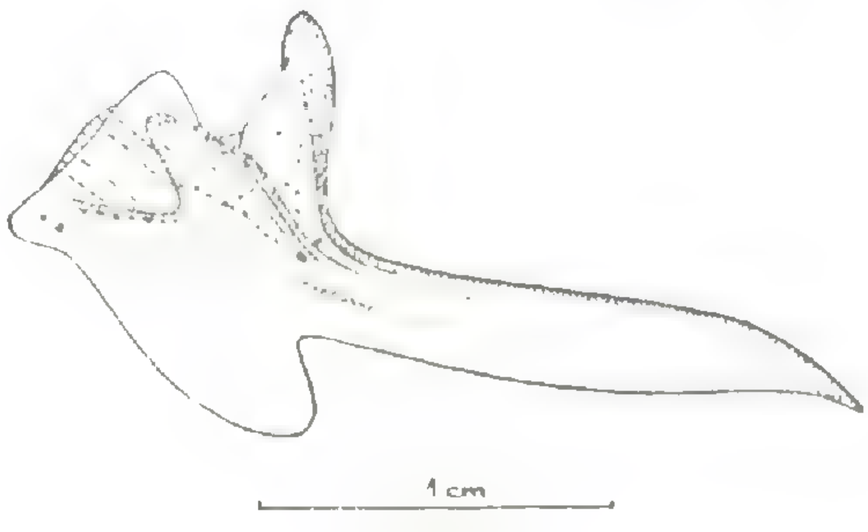
EXPLANATION OF THE ILLUSTRATION

PLATE XIII. CAULARTHRON BICORNUTUM (*Hook.*) *Rafinesque*. Drawing of *Dunsterville 399* from Venezuela.

Drawn by G. C. K. DUNSTERVILLE

Plate XIII





tations or pits on lower surface of lip. Column short, with conspicuous fleshy wings; clinandrium oblique, obtuse. Anther terminal, operculate, incumbent, more or less globose, 2-celled: cells divided longitudinally. Pollinia 4, waxy, each with a granular-viscid appendage. Capsule ellipsoidal.

Caularthron: from the Greek, meaning "jointed stem," undoubtedly in reference to the persistent leaf-bases which lend to the elongated pseudobulbs the appearance of being jointed.

A genus occurring from Guatemala through Middle America, northern South America and Trinidad and Tobago. Two rather variable species are known.

Key to the species of Caularthron

A. Labellum 24–28 mm. longum, profunde trilobatum, lobis usualiter sinu conspicuo separatis; lobo mediano propie lanceolato vel elongato-lanceolato; lobis lateralibus ovato-oblongis. Folia oblonga vel oblongo ligulata, 7–25 (plerumque 12–20) cm. longa ×1.5–4.2 (plerumque 3–4) cm. lata.

1. *Caularthron bicornutum*

Aa. Labellum 11–14 mm. longum, saepissime inconspicue trilobulatum vel auriculatum vel aliquando subintegrum, lobis usualiter non sinu separatis; lobo mediano propie triangulari-ovato; lobis lateralibus parvis, vulgo auriformibus. Folia ligulato-lanceolata, 7–19 (plerumque 14–15) cm. longa×0.8–2.8 (plerumque 1–1.8) cm. lata.

2. *Caularthron bilamellatum*

ORIGINAL DESCRIPTION:

138. *Caularthron* R. (Stem jointed) Diff. *Epidendron*. Label. libero, ad basi alato glanduloso. Col. libera bialata dentata, anthera terminalis 4 pollen. *Caul. articulato, vaginato, bifolio, paucifloro*—Habit very irregular. Types 2 Sp. 1. *Caul. bicornutum*. Epid. do Hook. b. m. 3332. Bulbo cauliformis, fol. rad. ligul. retusis, scapo paucifl. label. trilobo, medio lanc. ac basi bicorne, petalis ellipt. acutis albis. Trinidad . . .

Caularthron bicornutum (*Hook.*) *Rafinesque* Fl. Tellur. 2 (1836 [1837]) 41.

Epidendrum bicornutum Hooker in Bot. Mag. (1834) t. 3332.

Diacrium bicornutum (Hook.) Bentham in Journ. Linn. Soc. 18 (1881) 312.
Diacrium amazonicum Schlechter in Beih. Bot. Centralbl. 42, Abt. 2 (1925) 108; Pabst in Arqu. Bot. Est. São Paulo 3 (1955) 125, t. 316.

COMMON NAME: *Virgin Mary; Virgin Orchid* (Trinidad and Tobago).

Pseudobulbs long-cylindric, terete, 10–30 cm. long, 2–6 cm. in diameter. Leaves 3–4, thick, oblong, usually quite obtuse to rounded, 6–20 (mostly 15–17) cm. long, 20–50 mm. wide. Flowers few to 20, 5.5–6 cm. wide; pedicel (with ovary) 3–5 cm. long. Sepals broadly ovate-lanceolate, bluntly short-acuminate, 25–32 mm. long, 15–18 mm. wide. Petals ovate, usually clawed, acutish, 22–28 mm. long, 20–23 mm. wide, upper margin usually with a conspicuous notch. Lip fleshy, as long as petals but narrower, deeply 3-lobate, basally with triangular tooth on each side; lateral lobes elliptic-ovate, rounded; mid-lobe oblong, obtuse-acuminate; disk above with 2 erect, triangular, plate-like, obtuse, hollow projections near middle. Column 14–15 mm. long.

The type of *Caularthron bicornutum* was collected in Trinidad by Bradford, who wrote on the label: "This most beautiful species is found in the greatest abundance on the coast and on the adjacent islands at the Boca de Moros, Trinidad.—The rocks and trunks of decaying trees are in some places covered with it. This specimen was gathered on Gaspare Island March 12, 1846 on my return from an expedition to the coast of Venezuela. It flowers especially in the early part of the year from January to April."

The culture of *Caularthron bicornutum* requires a rather warm greenhouse with high humidity (Warner, R. & B. S. Williams: Orch. Alb. 4 (1885) t. 157; Rolfe,

R. A.: Gard. Chron. 2 (1887) 44; Lindenia 7 (1891) 19; Linden, L.; Orch. Exot. (1894) 752). Much difficulty has sometimes been experienced in establishing the plant, as the pseudobulbs, although large and apparently rather tough, seem to damage easily. Once established, it seems to thrive well under cultivation, especially if not disturbed. The most recent article dealing with its culture (Schairer, J. F.: Bull. Am. Orch. Soc. 24 (1955) 106, t. p. 107) states: "Plants are grown potted firmly in brown osmunda. During autumn and winter, when the plants are in active growth, they require a warm spot (night minimum 63° F if possible), high humidity and good light (as much or more than most Cattleyas) with plenty of water at the roots, and they appreciate supplemental feeding. At blooming time, they prefer a cooler spot and less light and moisture. They never require a severe rest period after blooming but are kept somewhat dry for a few months before new growth begins. They are native of the West Indies and the Guianas, where they often grow on bare rocks and tree trunks near the sea where they get plenty of moisture and cooling breezes during hot weather. Propagation is by division and they never propagate fast enough to supply the insistent demands of your friends."

Caularthron bicornutum and *C. bilamellatum* occupy rather clearly defined geographic areas: the former is native to South America north of the Amazon River and to Trinidad and Tobago, whereas the latter occurs in Middle America, along the northernmost rim of South America and in Trinidad. It is in Trinidad chiefly that the two species are contingent, but here there appears to be an ecological delimitation of the two species—*Caularthron bicornutum* forms a conspicuous element along and near the sea coast, while *C. bilamellatum* is known only from inland districts.

There are a number of minor morphological characters which serve to distinguish *Caularthron bicornutum* from *C. bilamellatum*. The former is, in general, a much larger and more robust plant than the latter and has flowers approximately twice as large. This difference is variable, and the specimens of *Caularthron bicornutum* from British Guiana are notably smaller in habit and flowers than those from other parts of the range of the species.

Caularthron bicornutum may be recognized at once through its deeply trilobate lip. The mid-lobe is characteristically lanceolate or elongate-lanceolate with the apical portion either long- or short-acuminate. The lateral lobes, which are ovate-oblong and either obtuse or subacute, are usually separated from the mid-lobe by a deep sinus. *Caularthron bilamellatum*, on the contrary, usually has an inconspicuously trilobulate or auriculate lip, the mid-lobe of which, characteristically triangular-ovate and acute, is not separated from the small, auriform lateral lobes by a recognizable sinus. To be sure, several collections are known from Trinidad which show a somewhat intermediate lobation of the lip, and here there may be evidence of hybridization. When the available material of these two species from their entire geographic ranges is taken into consideration, however, the significance of the shape of the lip as indicative of a possible evolutionary trend may be appreciated.

A convenient character for separating *Caularthron bicornutum* from *C. bilamellatum*—and a character which seems to have been overlooked—is found in the peculiar notching of the upper margin of the petals of *C. bicornutum*. This margin, which faces the dorsal sepal, usually has one conspicuous notch situated one-third or one-half of the distance from the base of the petal. In some of the specimens, the notch is sharp and triangular; in others, it is less clearly defined. In all cases, however,

the presence of this notch causes the marginal area of the petal to be somewhat ruffled or crumpled. I have very rarely observed anything similar to this condition in *Caularthron bilamellatum*.

In the general shape of the hollow processes or "horn-like calluses" which arise from the disk of the lip and which have been used as the outstanding generic character, there is evident little variability from specimen to specimen, albeit some variation in relative size may be seen. Similarly, there is no significant morphological difference between these processes in *Caularthron bicornutum* and *C. bilamellatum*.

Unlike the concept *Caularthron bilamellatum*, *C. bicornutum* does not have a large synonymy. This is due partly, perhaps, to the greater variability in the former than in the latter species.

In 1925, Schlechter described *Diacrium amazonicum* from material collected in Brazil. The type material of *Diacrium amazonicum* is no longer extant, but a study of the type description convinces me that Schlechter specified no differences which, with the material at hand today, we could not easily accommodate in *Caularthron bicornutum*. Pabst (loc. cit.) determined a specimen (*Frões 21541*) from the Rio Negro in Amazonian Brazil as representing *Diacrium amazonicum* and published a diagnostic drawing of the floral parts. This drawing likewise shows no character which could serve to distinguish the plant from *Caularthron bicornutum*.

TYPE COLLECTION: Cult. Hort. Wentw[orth], from Trinidad (Herb. Kew).

CULTIVATED: (Herb. Rchb. 898); Hort. Rucker, May 27, 1840 (Herb. Rchb. 899; Herb. Ames 69096a); "from the type plant of Gard. Chron. 1887, pt. 2, p. 45, fig. 11," Hort. Kew, May 1887, *R. A. Rolfe s.n.* (Herb. Kew); Botanic Station, Grenada, W.I. "Originally from Trinidad," April 14, 1906, *W. E. Broadway s.n.* (Herb. Ames 7906, 7907).

Brazil: Estado do Amazonas, Manáos, *Spengler s.n.* (Herb. Rchb. 896); Estado do Amazonas, Rio Negro, December 21, 1945, *R. L. Fróes 21541* (Record in Herb. Ames of specimen in Herb. Inst. Agron. Norte).

British Guiana: "Flowers white, pink towards the apex, labellum pink with a yellow disk." 1837, *R. Schomburgk 429* (Herb. Kew; Herb. Field Mus. 1025283); Banks of Corentyne River near Crealla, September 1879, *E. F. im Thurn s.n.* (Herb. Kew); Essequibo River, December 1886, *Jenman 3590* (Herb. Kew); *Jenman 7761* (Herb. Kew); Hort. Kew, May 1889 (Herb. Kew); Mount Roraima, Autumn 1894, *J. J. Quelch & F. McConnell 280* (Herb. Kew); *C. F. Appun 657* (Herb. Kew); Cuyuni River, islet at the Akaio Falls. "Epiphyte at about 15 feet; roots in dense clusters. Fl. shallow, cup-shaped, like an *Anthericum*, pedicels mauve. Fl. resupinate. Pets. and sep. pure white, with striations. Stele at base and all labellum spotted with purple. Humps of label. and depression between them and stele yellow, spotted with purple. Label. otherwise white." November 25, 1929, *N. Y. Sandwith 685* (Herb. Kew).

Colombia: Comisaría del Vaupés, Río Negro, El Castillo (San Felipe). "Flowers white, sepals delicately pink-tinged. Lip yellow, spotted brown. Very fragrant." December 12, 1947, *R. E. Schultes & F. López 9335a* (Herb. Ames 67526, 67527).

Tobago: *G. W. Meyer* (?) *s.n.*, December 1879 (Herb. Kew); Roxborough Bay, Military Road, "growing on the stems of logwood tree," February 2, 1879, *G. W. Meyer s.n.* (Herb. Kew); Bacolet, "on rocks and trees near the sea, flowers white with a few purplish spots, very fragrant," January 20, 1910, *W. E. Broadway s.n.* (Herb. Gray 4278); Rockley Vale, "on trees, *Virgin Mary*," February 20, 1913, *W. E. Broadway s.n.* (Herb. Gray 4277; U.S. Nat. Herb. 759445); February 19, 1932, *D. Fairchild 2930* (U.S. Nat. Herb. 1625959; Herb. Ames 69057).

Trinidad: *Borroughs s.n.* (?) (Herb. Rchb. 896); *Bradford 1845* Herb. [Hance 5332] Herb. Kew); Gasparee Island, "on rocks and trees overhanging the sea," December 30, 1906, *W. E. Broadway s.n.* (Herb. Ames 10085, 10086, 10087, 10088, 10089, 68642; Herb. Field Mus. 464601); Maraval, "on rocks and trees," February 3, 1911, *W. E. Broadway s.n.* (Herb. Kew; Herb. Ames 69058); Moruga sea shore, Lance Mettan. "On shrubs, trees and rocks." February 9, 1916, *W. E. Broadway s.n.* (Herb. Trin. 7595; Ames 69924); "On a tree," May 26, 1918, *W. E. Broadway s.n.* (Herb. Ames 22062; Herb N. Y. Bot. Gard.); Manzanilla, "Flowers white. On a fallen tree," March 9, 1921, *N. L. Britton & E. G. Britton 2173* (Herb. N.Y. Bot. Gard.; U.S. Nat. Herb. 1198102); Little Gasparee, April 4, 1921, *N. L. Britton 2659* (Herb. N.Y. Bot. Gard.); Chacachacare,

January 5, 1922, *W. E. Broadway s.n.* (Herb. Trin. 10566, 2 sheets); Herb. Ames 69925); St. Ann's (Cult.) "wild on rocks and trees along sea shores," March 3, 1923, *W. E. Broadway s.n.* (Herb. Field Mus. 549522); Between Balandra and Toco, "rocks by shore," February 2, 1926, *W. G. Freeman s.n.* (Herb. Trin. 11519); Balandra Bay, "on rocks and low trees near the sea shore. *Virgin Orchid*," February 22, 1931, *W. E. Broadway s.n.* (U.S. Nat. Herb. 1519971; Herb. Mo. Bot. Gard. 1005390); "On trees and rocks, sea shore districts: *Virgin Orchid*," February 23, 1934, *W. E. Broadway s.n.* (Herb. Ames 40385; Herb. Kew); Quinam Bay, St. Patrick, "On trunk of tree, fls. white with faintly speckled throat," January 30, 1946, *L. H. Bailey 121* (Herb. Ames 62541); Chacachacare Island, January 20, 1956 [*Capt. Mendez*] *W. G. Downs & T. H. G. Aitken 15f* (Herb. Ames Alc. Coll. 3187); Sangre Grande, Rio Grande Forest Tree Station, $1\frac{1}{4}$ mile from coast, March 7, 1956, *W. G. Downs & T. H. G. Aitken 15g* (Herb. Ames Alc. Coll. 3183); Chachachacare Island, seacoast, January 14, 1957 [*A. S. Fenwick*] *W. G. Downs & T. H. G. Aitken 15c* (Herb. Ames Alc. Coll. 3204a); Vega de Oropouche, 1 mile from sea, *W. G. Downs & T. H. G. Aitken 15a* (Herb. Ames Alc. Coll. 3206a).

VENEZUELA: [Drawing of a flowering specimen] Carabobo, alt. 2500 ft., 1851 (Herb. Rchb. 890; Herb. Ames 69098); Paria Peninsula, Cariaquita, January 16–21, 1911, *F. E. Bond, T. S. Gillin & S. Brown 40* (Herb. N.Y. Bot. Gard., U.S. Nat. Herb. 1189830); vicinity of Cristóbal Colon, January 5–February 22, 1923, *W. E. Broadway 337* (Herb. Gray 4275; Herb. N.Y. Bot. Gard.; U.S. Nat. Herb. 1187925, 1197666); vicinity of Cristóbal Colon, Avicana, January 5–February 22, 1923, *W. E. Broadway 616* (Herb. Gray 4276; U.S. Nat. Herb. 1197675); April 29, 1941, *H. Pittier s.n.* (Herb. Ames 68209); [Drawing of a flowering specimen] *G. C. K. Dunsterville 399* [*Arrigo R. s.n.*], Puerto Ayacucho (Herb. Garay 6358).

Caularthron bilamellatum (*Rchb.f.*) *R. E. Schultes comb. nov.*

Epidendrum bilamellatum Reichenbach fil. in Walpers Ann. Bot. 6 (1862) 345.

Epidendrum bigibberosum Reichenbach fil. loc. cit. 8 (1862) 346.

Epidendrum indivisum Bradford ex Grisebach Fl. Brit. W. Ind. Isl. (1864) 614.

Diacrium bigibberosum (Rchb.f.) Hemsley in Godman & Salvin Biol. Centr.-Am., Bot. 3 (1883) 222.

Diacrium bilamellatum (Rchb.f.) Hemsley in Godman & Salvin loc. cit. 222.
Diacrium indivisum (Bradf. ex Griseb.) Broadway in Bull. Misc. Inform. Trinidad 2 (1895) 79.
Diacrium bicornutum (Hook.) Bentham var. *indivisum* (Bradf. ex Griseb.) Cogniaux in Martius Fl. Bras. 3, pt. 5 (1898) 188.
Diacrium venezuelanum Schlechter in Fedde Repert. Sp. Nov. Beih. 6 (1919) 41.
Diacrium bilamellatum (Rchb.f) Hemsley var. *Reichenbachianum* Schlechter loc. cit. 17 (1922) 47, *in textu*.
Diacrium bivalvatulum Schlechter loc. cit. 19 (1923) 123.

Pseudobulbs subcylindric to long-fusiform, terete, 5–23 cm. long, up to 4 cm. in diameter. Leaves 2–3, ligulate-lanceolate to linear-oblong, obtuse, 5–22 cm. (mostly more or less 15) cm. long, 6–25 mm. wide. Inflorescence erect, up to 15 cm. long. Flowers white or white tinged with pink or lavender, few to numerous, up to about 3 cm. wide; pedicel stout, (with ovary) 1.5–2.5 cm. long. Bracts triangular, cucullate, acute, up to 5.5 mm. long. Sepals concave, elliptic-ovate, acute or sometimes subobtuse and apiculate; dorsal sepal 12–17.5 mm. long, 6 mm. wide; lateral sepals 10–16 mm. long, 6–8 mm. wide. Petals short-clawed, elliptic-obovate to broadly obovate, acute or subobtuse, 10–16 mm. long, 6–9 mm. wide. Lip fleshy, as long as petals, subentire to more or less 3-lobulate; lateral lobes small and auriculate, sometimes only tooth-like, usually without a sinus; mid-lobe triangular-ovate, apically short- or long-acute; disk above with 2 large, erect, triangular, plate-like, obtuse, hollow projections. Column 8–11 mm. long. Capsule up to 2.8 cm. long.

The type of *Epidendrum bilamellatum* was collected in "Caracas" (referring probably to a very extensive area

EXPLANATION OF THE ILLUSTRATION

PLATE XIV. CAULARTHRON BILAMELLATUM (*Rchb.f.*) *R. E. Schultes.* 1, flowering and fruiting plant, one third natural size. 2, flower, approximately natural size. 3, column and lip, side view, almost twice natural size.

Drawn by GORDON W. DILLON

Plate XIV

in Venezuela and not specifically to the city), Venezuela, by Wagener and is preserved in the Reichenbach Herbarium on sheet No. 891. This sheet, which is labelled "*Epid. bicornutum*" has, pasted on a card attached to the sheet, three flowers from *Fendler 2436*, collected near Colonia Tovar in Venezuela in 1856–1857. This Fendler material, representing *Caularthron bilamellatum*, has been given the number of Herb. Reichenbach 891a in order to distinguish it from the type or Wagener collection. There are also, pasted on the sheet with the type, two labels indicating that the collection was made by Linden in "Nouvelle Granade," but since the original handwritten label is obviously the correct one, we must assume that, as so often happened, the printed Linden labels were glued to the sheet at a subsequent date and undoubtedly in error.

An examination of the type material of *Epidendrum bigibberosum* (Herb. Reichenbach 893, 894) and of Reichenbach's diagnostic sketches of the floral parts fails to uncover a single character which might serve to distinguish this collection from the type of *E. bilamellatum*. In his original description of the concept *Epidendrum bigibberosum*, Reichenbach likewise failed to point out any differences. We, therefore, must reduce *Epidendrum bigibberosum* to synonymy under *Caularthron bilamellatum*.

For some time, I have been undecided as to what the concept which has been known as *Diacrium indivisum* (*Epidendrum indivisum*) really represented. Bradford drew up a description based on one of his Trinidad collections, and this was published as *Epidendrum indivisum* by Grisebach. It was transferred to *Diacrium* by Broadway in 1895. Cogniaux maintained that the concept represented a variety of *Diacrium bicornutum* and made the necessary nomenclatural adjustment. In 1956, I pub-

lished a note indicating my belief that there seemed to be sufficient morphological evidence to maintain it [*Diacrium indivisum*] as specifically distinct from the only other Trinidad representative of the genus. Subsequently, when Dr. Wilbur G. Downs sent me from Trinidad photographs and additional material of the two concepts of *Caularthron* known to grow on the island, I began to realize that a revision of the genus *Diacrium* was necessary before a clear understanding of the Trinidad material could be expected.

The type specimen of *Epidendrum indivisum* is preserved at Kew, together with Bradford's handwritten description of the concept. The type bears the annotation "Herb. Hance 5334." On the same sheet with the type there are pasted two inflorescences from plants collected in Trinidad and flowered at Kew in May 1889. Rolfe has annotated this collection as "*Epidendrum bicornutum* var. cleistogamic flowers=*D. indivisum.*"

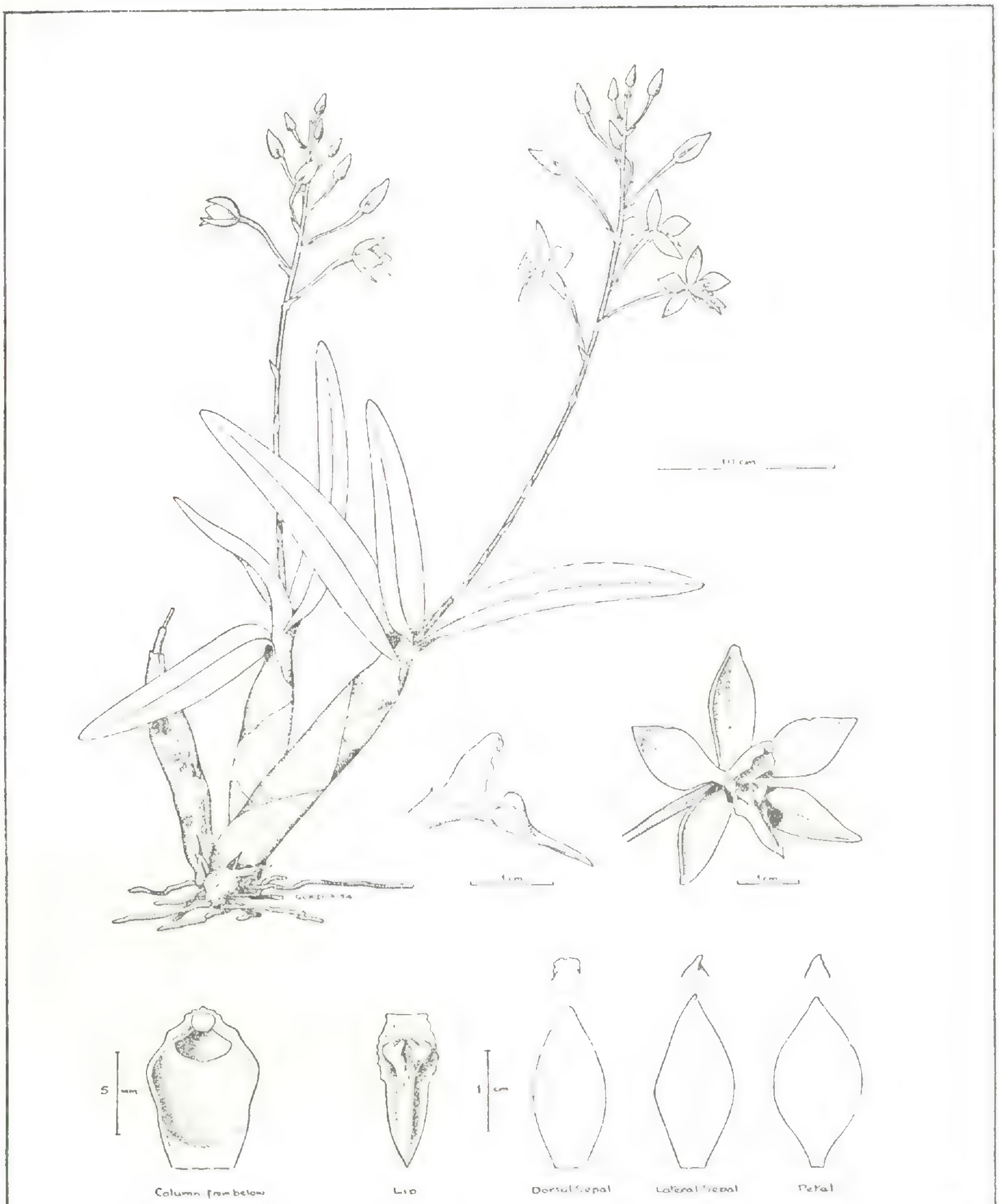
According to Bradford's manuscript description, the type has an undivided lip. In the published description, the lip of the type was stated to be "undivided or minutely auricled above the base." The apical part of the lip was described as "acuminatum" in the manuscript and "subulate-lanceolate" in Grisebach's *Flora*. Unfortunately, the type has, at the present time, only two buds and one imperfect flower. We know from later material, however, that, in Trinidad, this concept is often cleistogamous. It is possible that the type flowers may have been peloric. At least, we do know from the material now available from Trinidad that the lip is very rarely entire but is most often laterally auriculate at the base or inconspicuously bilobulate. In this, as in other respects, the concept does not depart from *Caularthron bilamellatum*, of which it is, consequently, here designated as a synonym.

EXPLANATION OF THE ILLUSTRATION

PLATE XV. CAULARTHRON BILAMELLATUM (*Rchb.f.*) *R. E. Schultes.* Drawing of *Dunsterville 181* from Venezuela.

Drawn by G. C. K. DUNSTERVILLE

Plate XV


10 cm
1 cm
1 cm
5 mm
1 cm
Column from below
Lip
Dorsal Sepal
Lateral Sepal
Petal

Schlechter's *Diacrium venezuelanum*, a record of the type of which is preserved in the Ames Herbarium, shows no character which cannot fall easily within the variability of *Caularthron bilamellatum*. *Diacrium bivalvatulum*, likewise, presents, according to Schlechter's original description, no differences of sufficient importance for the maintenance of it as a distinct species. *Diacrium venezuelanum* and *D. bivalvatulum* are, therefore, placed in synonymy under *Caularthron bilamellatum*.

TYPE COLLECTION: Venezuela, "Caracas," *Wagener s.n.* (Herb. Rchb. 891; Herb. Ames 69055).

COLOMBIA: 1842, *Sinclair s.n.* (Herb. Kew).

BRITISH HONDURAS: *W. A. Schipp S-482* (Herb. Ames 40443).

COSTA RICA: [Drawing of a flowering specimen and diagnosis of flower] Punta Arenas, February 1909, *A. & C. Brade 1265* (TYPE of *D. bivalvatulum*); Provincia de Alajuela, El Coyolar, alt. about 240 m. "On tree; bulbs elongate, full of ants." April 1–3, 1924, *P. C. Standley 39982* (Herb. Ames 29865); Golfo Dulce, Playa Blanca, sea level, February 25, 1933, *M. Valerio 553* (Herb. Field Mus. 893155).

GUATEMALA: Cult. Hort. Shiller, from Guatemala, *Skinner 1458* (TYPE of *E. bigibberosum*, Herb. Rchb. 893, 894; Herb. Ames 24081, 69091); Montufor Flats, February 27, 1939, *M. W. Lewis 217* (Herb. Ames 69926); Departamento de Izabál, between Milla 49.5 and Cristina, alt. 65–70 m. "On limbs of tree along wooded margins of prairie. Pseudobulb terete, pale green. Leaves thick, coriaceous, rich olive-green. Stem olive-green with purple suffused above and at nodes. Pedicels purplish. Buds orchid-colored. 3 outer sepals delicate orchid without, white within. 2 petals white. Lip white on upper petal and stigma and white on beak with pale orchid color along edge or the column with more lavendar." *J. A. Steyermark 38389* (Herb. Field Mus. 1043049); Departamento de Izabál, Bay of Santo Tomás, between Escobas and Santo Tomás, alt. sea level to 2 m. April 13, 1940, *J. A. Steyermark 39341* (Herb. Field Mus. 1041145; Herb. Ames 63752); Departamento de Izabál, shores of Lago Izabál, opposite San Felipe; between San Felipe and mouth of Río Juan Vicente, alt. 50 m. April 19, 1940, *J. A. Steyermark 39692* (Herb. Field Mus. 1035306).

PANAMA: Santa Rita Trail, February 27, 1905, *J. F. Cowell 160* (Herb. N.Y. Bot. Gard.); Cultivated from Canal Zone, Culebra, alt. 50–100 m., April 8, 1911, *H. Pittier 3406* (Herb. Ames 21797); Patiño, southern Darien, "on cliffs along the beach," February 13, 1912, *H. Pittier 5706* (Herb. N.Y. Bot. Gard.; U.S. Nat. Herb.

715996); Canal Zone, Balboa. "Never flowers a full spray. It is necessary to pick a flower at a time as they show." [rec'd] May 4, 1923, *C. W. Powell 67* (Herb. Ames 23965, 23966, 69927; Herb. Ames Alc. Coll. 438; Herb. Mo. Bot. Gard. 955922); Canal Zone, Fort Sherman, January 15, 1924, *P. C. Standley 31231* (U.S. Nat. Herb. 1225409); Provincia de Panamá, between Matías Hernández and Juan Díaz, January 21, 1924, *P. C. Standley 31944* (U.S. Nat. Herb. 1225418); Provincia de Panamá, swamp between El Jagua Hunting Club on Río Jagua and El Congor Hill, alt. 2 m., February 10, 1935, *A. A. Hunter & P. H. Allen 473* (Herb. Ames 42248); Pearl Islands, Trapiche Island, March 15, 1937, *G. S. Miller 1908* (U.S. Nat. Herb. 1688731); Pearl Islands, San José Island, March 16, 1937, *G. S. Miller 1909* (U.S. Nat. Herb. 1688746) Isla Colon, April 1, 1940, *H. von Wedel s.n.* (Herb. Mo. Bot. Gard. 1227010); Provincia de Bocas del Toro, vicinity of Chiriqui Lagoon, Old Bank Island, "flowers purplish," February 15, 1941, *H. von Wedel 2100* (Herb. Ames 61530; U.S. Nat. Herb. 1863094); Perlas Archipelago, Gulf of Panamá, San José Island (mouth of Mata Puerco), about 55 miles southeast of Balboa, April 12, 1945, *I. M. Johnston 703* (Herb. Ames 64953).

TRINIDAD: Cult. Hort. Trin. from "Inland Districts" *J. H. H[art] s.n.* (Herb. Trin. 5512); Inland Woods, 1896, *J. H. H[art] s.n.* (Herb. Trin. 5983; Herb. Kew; Herb. Ames 66910, 68215); *Bradford s.n.* [Herb. Hance 5334] (TYPE of *E. indivisum*, Herb. Kew); Cult. Hort. Kew from Trinidad, May 1889 (Herb. Kew); Government House Grounds, June 3, 1907, *W. E. Broadway s.n.* (Herb. Ames 10736); Government House Grounds. "Flowers white," June 22, 1907, *W. E. Broadway s.n.* (Herb. Ames 10727); Erin, March 27, 1908, *W. E. Broadway s.n.* (Herb. Ames 10640); Santa Cruz, February 23, 1912, *W. E. Broadway s.n.* (Herb. Kew; Herb. Mo. Bot. Gard. 918485); St. Augustine, Imperial College of Tropical Agriculture, April 15, 1949, *N. W. Simmonds 351* (Herb. Trin. 14438; Herb. Ames 66931); St. Augustine, 6 miles from sea, *W. G. Downs & T. H. G. Aitken 15b* (Herb. Ames Alc. Coll. 3205a); Caigual, about 4 miles from coast, January 24, 1955, *W. G. Downs & T. H. G. Aitken 15e* (Herb. Ames 67831, 67783); Plain Road, 3–4 miles from sea, January 14, 1957, *W. G. Downs & T. H. G. Aitken 15d* (Herb. Ames Alc. Coll. 3203a).

VENEZUELA: Near Colonia Tovar, 1856–1857, *A. Fendler 2436* (Herb. Rchb. 891a; Herb. Kew; Herb. Gray 4077); [Drawing of flowering specimen and floral diagnosis] Cult. Hort. K. W. John, flowered June 1904, from Venezuela (TYPE of *D. venezuelanum*, Herb. Ames 69928); Between Valencia and Maracay, January 31, 1918, *H. Pittier 7748* (U.S. Nat. Herb. 987846); Rastrojos, near Cabudare, Lara, Decem-

ber 1923, *J. Saer 116* (U.S. Nat. Herb. 1193211); June 1939, *V. Barnes 5923* (Herb. Ames 58216).

Excluded or uncertain concepts

Diacrium bidentatum (*Lindl.*) *Hemsley* in Godman & Salvin Biol. Centr.-Am., Bot. 3 (1883) 221.

Epidendrum bidentatum Lindley Gen. and Sp. Orch. Pl. (1831) 98.

The type of *Epidendrum bidentatum* is preserved in the British Museum. Study of a photograph of the type and diagnostic sketches in the Ames Herbarium indicates that this concept cannot be referred to *Caularthron*, but that, without a doubt, it represents, as has previously been suggested (Williams, L. O. in Ceiba 2 (1951) 174), *Epidendrum Boothianum* Ldl.

Diacrium Ulmckei *Kränzlin* Mitteil. Inst. Allg. Bot. Hamb. 6 (1927) 419.

This concept was described on the basis of material which flowered in the Hamburg Botanical Garden. The plant had presumably been collected in Guatemala. Since the Hamburg Herbarium has apparently disappeared, we are unable to trace a type, if indeed an herbarium specimen were ever preserved there when the concept was described. After an examination of the description, I rather doubt that the concept can be accommodated in the genus *Caularthron*.

STUDIES IN AMERICAN ORCHIDS III[1]

A new Genus from the Colombian Amazonia

BY

LESLIE A. GARAY[2]

TIME and again, the interpretation of orchid genera has caused grave problems, since we often find that many of the species which are assigned to a particular genus are either atypical or obviously do not belong to the concept in question. Recently, I encountered a problem of this nature, which I wish to discuss here.

In 1934, Mansfeld described *Hybochilus Huebneri*, which he based on a collection sent in by Mr. Huebner from the Amazon region of Colombia. At first, it appeared to him that this collection might represent a new generic concept, but for some unknown reason he finally decided to include it in the genus *Hybochilus*. This species has subsequently been all but unknown, and its nomenclatorial type was destroyed during the Second World War.

While studying a number of collections from Colombia in the Ames Herbarium, I found two undetermined specimens which appeared to be quite peculiar in their

[1] Previous numbers of this series were published in the Canadian Journal of Botany, vol. 34: (1956), pp. 241–260, 721–743.

[2] Assistant Curator of the Herbarium, Department of Botany, University of Toronto, Toronto, Canada; at present, a Guggenheim Fellow at the Orchid Herbarium of Oakes Ames, Harvard University.

general habit and which immediately suggested *Quecketia*, another genus of the subtribe *Capanemieae* and known only from the Guianas. I consequently investigated all of the genera and species of the *Capanemieae*, and I am now convinced of the identity of my material with that of the concept *Hybochilus Huebneri*.

According to Schlechter's system, such features as an incumbent anther and auricles which are a continuation of the clinandrium characterize the *Capanemieae*. A completely dorsal anther and the presence of auricles on the column which enfold the stigmatic cavity are characters of the monogeneric subtribe *Papperitzieae;* these characters are clearly observable in *Hybochilus Huebneri*. The structure of the column, however, is much more complicated than in *Papperitzia*. There are two pairs of lobes: one pair is located in front of the column, with their parallel sides enclosing the stigma, the lower margins being completely connate to form a shallow, cup-like cavity immediately beneath the stigmatic surface; the other pair of lobes terminate the column. At first, these are parallel and enclose the lower portion of the anther. When the anther is removed they open up slightly and become spirally twisted. It is hard to state the real function of these lobes, since we have no field observations. It appears, however, that so long as the flowers are not visited by pollinating insects they remain fairly connivent, but after the removal of pollinia they open up slightly. I believe that these auricles protect the viscosity of the stigma and pollen-gland from rapid desiccation.

In view of these dissimilarities, which I consider to be of basic importance in the differentiation of subtribes as well as of genera within the subtribes, I believe that *Hybochilus Huebneri* represents a distinct genus which should be placed in the *Papperitzieae*.

Polyotidium *Garay gen. nov.*[3]

Sepalum posticum a sepalis lateralibus omnino liberum, valde concavum; sepala lateralia usque ad medium connata, basi leviter saccata. Petala plana, sepalo postico subsimilia. Labellum basi columnae adnatum, non articulatum; hypochilum late excavatum, epichilum cuneato-flabellatum, planum. Columna apoda, brevis, paulo arcuata, apicem versus leviter dilatata, alis quaternis ornata; alae duae inferiores in facie columnae juxta orificium stigmaticum patentes, superiores duae in apice columnae erectae. Orificium stigmae ellipticum, valde concavum. Rostellum valde conspicuum, alte bifidum. Clinandrium posticum, vix rite evolutum, integerrimum. Anthera dorsalis, dehiscens, in medio columnae inserta, erecta, ovato-oblonga, unilocularis. Pollinia 2, subglobosa, stipites longi angustissimi, glandula obovato-triangula. Herbae epiphyticae, habitu *Quekettiam microscopicam* in mentem revocans. Pseudobulbi parvi, unifoliati. Folia lineari-subulata, carnoso-coriacea. Inflorescentiae laterales, simplices vel pauciramosae. Flores parvi, distincte pedicellati.

Genus monotypica e regione Amazonicae Colombianae.

Polyotidium Huebneri (*Mansf.*) *Garay comb. nov.*

Hybochilus Huebneri Mansf. in Fedde Repert 36: (1934) 61.

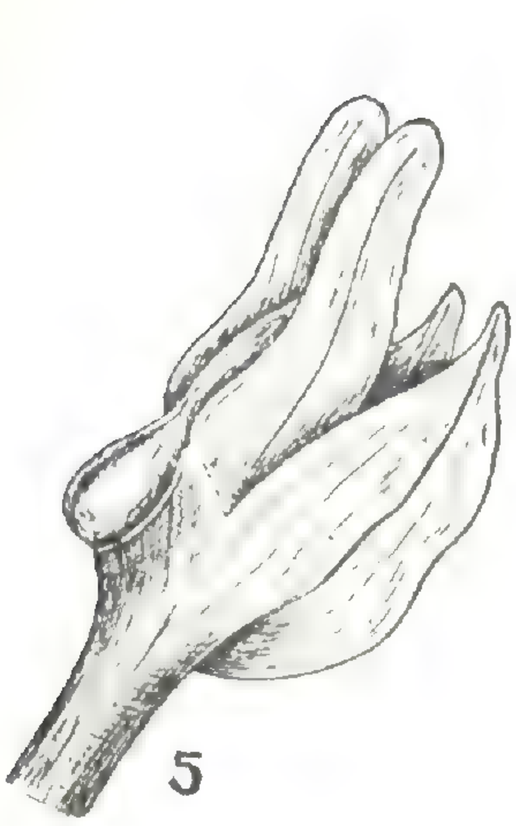
Epiphytica, caespitosa, usque ad 20 cm. alta; radicibus filiformibus, leviter flexuosis, glabris; pseudobulbis anguste cylindraceis, unifoliatis vaginis 3, scariosis, acutis vel brevissime acuminatis omnino vestitis; folio subuliformi, carnoso-coriaceo, erecto vel leviter arcuato, 12–19 cm. longo, 2–3 mm. in diametro; inflorescentia e basi

[3] **Polyotidium:** *poly* = many; *otion* = small ear, in allusion to the several auricles present on the column.

EXPLANATION OF THE ILLUSTRATION

PLATE XVI. POLYOTIDIUM HUEBNERI (*Mansf.*) *Garay*. 1, plant, three quarters natural size. 2, lateral sepals, four times natural size. 3, petal, five times natural size. 4, lip, five times natural size. 5, column, lateral view, nine times natural size. 6, column, front view, eight times natural size. 7, pollinia, greatly enlarged. 8, anther, greatly enlarged.

Plate XVI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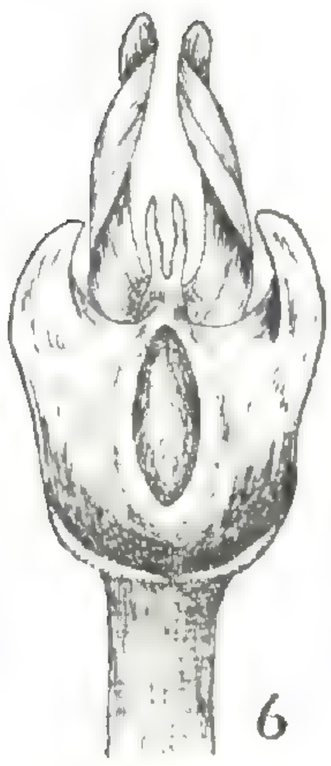
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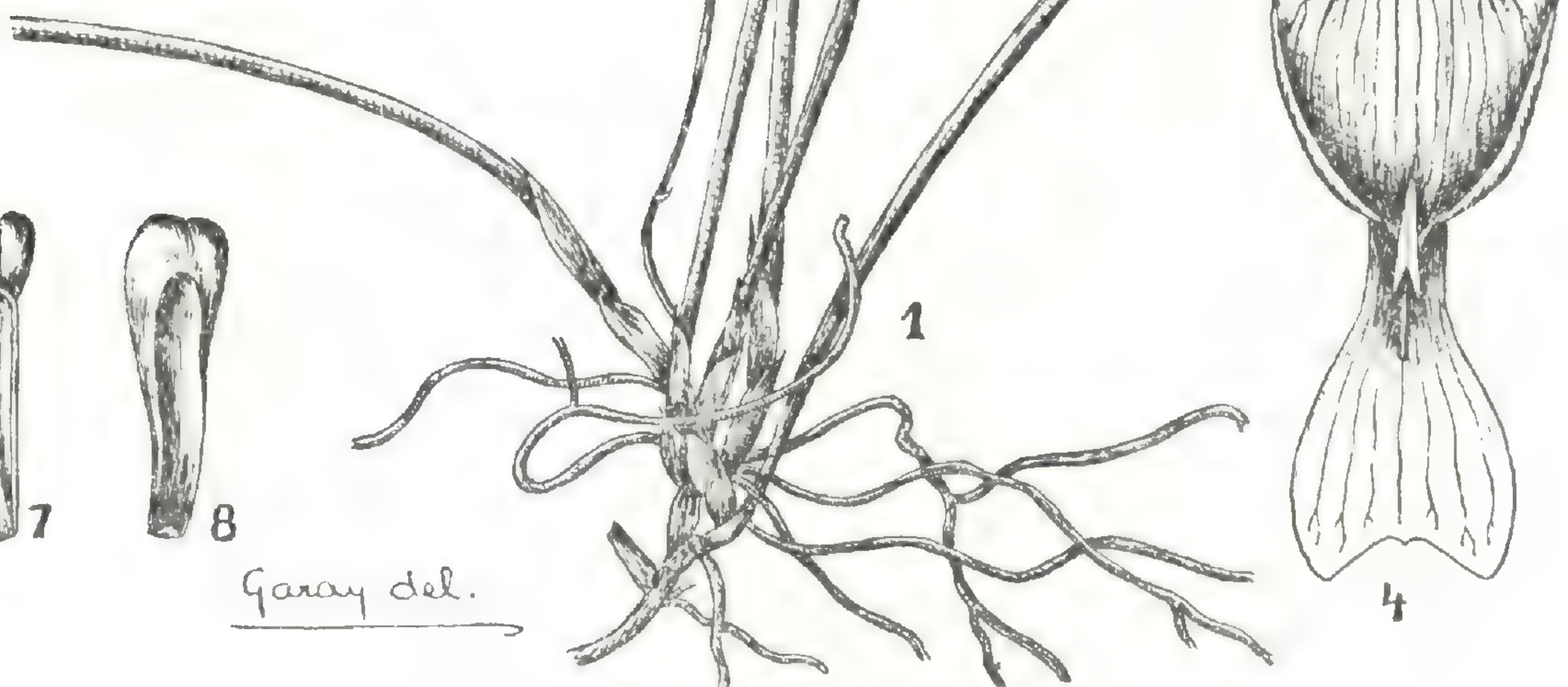
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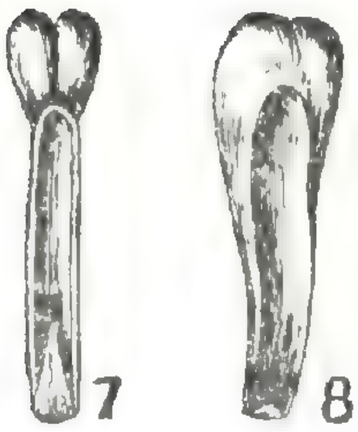
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Garay del.

pseubobulborum simplici vel pauciramosa, laxe pluriflora, 9–16 cm. longa; bracteis lanceolatis, ovariis pedicellatis multoties brevioribus, 2 mm. longis: sepalo postico elliptico, valde concavo, 3-nervio, apice acuto, 6–8 mm. longo, 2.5–3 mm. lato; sepalis lateralibus usque ad medium connatis, lanceolato-ellipticis, apice acutis et inter se divergentibus, basi leviter saccatis, 3-nerviis, ca. 7–8 mm. longis, supra basin 3.5–4 mm. latis; petalis late ellipticis, acutis, 5-nerviis, 7–8 mm. longis, 3–4 mm. latis; labello sessili, basi columnae adnato, in medio constricto, 9–10 mm. longo; parte basilari (i.e. hypochilo) subglobosa, valde concava, ad basin utrinque callo minuto, globoso ornata, epichilo plano, cuneato-flabellato, antice emarginato cum apiculo; disco in medio ad constructionem callis 2 approximatis donato; columna apoda, 4-auriculata, 5–6 mm. alta; ovario cylindraceo, pedicello incluso 4–6 mm. longo.

Huebner 226 was originally designated as the type of *Hybochilus Huebneri*, but it was destroyed during the Second World War. To the best of my knowledge, the two collections in the Ames Herbarium cited below constitute our only representation of this concept. Since this species is the basis of a distinct genus, it is essential to select a new nomenclatorial type, for which I hereby designate the excellent collection *Schultes & López 9300* (TYPE in Ames Herbarium No. 68524).

COLOMBIA: Comisaría del Vaupés, Río Negro basin, El Castillo, near confluence of Guainía and Casiquiare. Dec. 12, 1947. *Richard Evans Schultes & Francisco López 9300.* NEOTYPE: (Ames Herbarium No. 68524).—Comisarías del Amazonas y Vaupés: Río Apaporis, Raudal Jirijirimo (below mouth of Kananarí). Quartzite base, 900 ft. alt. Flowers vermillion. Jan. 21, 1952. *Richard Evans Schultes & Isidoro Cabrera 14960* (Ames Herbarium No. 68495).—Comisaría del Amazonas: La Pedrera. Feb. 1926. *G. Huebner 226* (ex Mansfeld).

A NEW LEPANTHOPSIS FROM VENEZUELA

BY

CHARLES SCHWEINFURTH

LIKE many other small, recently segregated genera, Lepanthopsis is now recorded as rather widespread in the American tropics from southern Florida, Central America and the West Indies into most of northern South America as far as Brazil and Peru. The following species is the first of its genus, however, to be described from Venezuela.

Lepanthopsis vinacea *C. Schweinfurth sp. nov.*

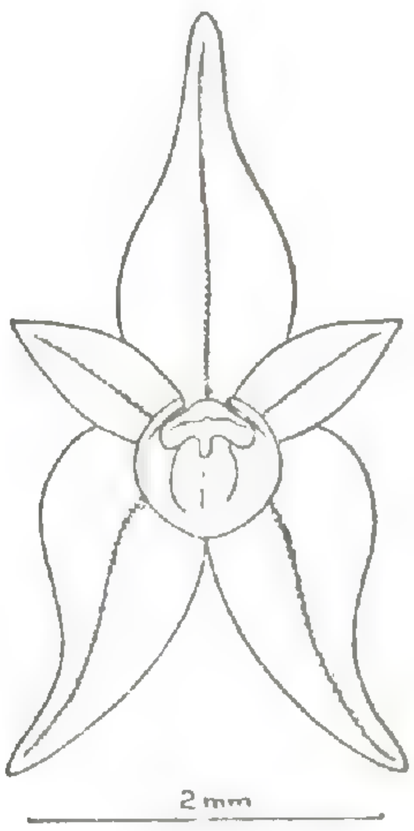
Herba gracilis, epiphytica, caespitosa. Caules tenues, vaginis tubulatis, lepanthiformibus, arctis omnino celati. Folium erectum, breviter petiolatum; lamina ovalis vel oblongo-elliptica, obtusa. Inflorescentiae axillares, singulae vel perpaucae, quam folium multo longiores, graciles, prope apicem densiflorae, cum floribus secundis, vinaceis. Flores parvi, membranacei, horizontales. Sepalum dorsale lanceolato-ovatum, superne abruptius angustatum. Sepala lateralia oblique ovato-lanceolata, basi connata, in partem superiorem acuminatam curvata. Petala sepalis multo minora, elliptico-ovata, acuta. Labellum quam petala brevius sed latius, in circuitu orbiculare cum auriculis retrorsis, triangulari-incurvis. Columna generis.

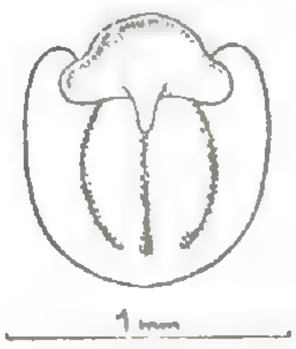
Plant small, slender, epiphytic. Roots fibrous, flexuous, glabrous, numerous. Stems simple, caespitose, slender, apically unifoliate, up to 5.7 cm. long, entirely concealed by several (up to 9) close, tubular, lepanthiform

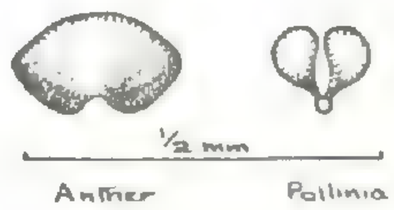
EXPLANATION OF THE ILLUSTRATION

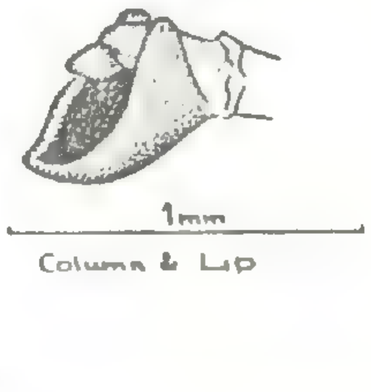
PLATE XVII. LEPANTHOPSIS VINACEA *C. Schweinf.*
Drawing of *Dunsterville 425* from Venezuela.
Drawn by G. C. K. DUNSTERVILLE

Plate XVII









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sheaths which are very minutely muriculate on the angles and terminate in a spreading, ovate, marginate, hispid mouth. Leaf erect, very shortly petioled, rather thick and fleshy; lamina oval to oblong-elliptic, obtuse, cuneate below, marginate, 15–21 mm. long, up to 9 mm. wide; petiole about 3 mm. long. Inflorescences axillary, 1–4 (rarely 6) to a stem, much surpassing the leaves, a single one floriferous at a time, suberect to flexuous or spreading, about 4.5–5 cm. long; peduncle filiform, with several, inconspicuous, remote, tubular sheaths; raceme densely secund-flowered, about 1–2 cm. long. Floral bracts minute, infundibuliform. Flowers few to numerous, horizontal, with widely spreading segments, deep wine-color or bright purple. Dorsal sepal lanceolate-ovate, rather abruptly narrowed to a subacute tip, 1-nerved, about 2–3 mm. long and 1–1.5 mm. wide. Lateral sepals similar, obliquely ovate-lanceolate, connate near the base, with outcurved, acuminate tips, about 2–3.2 mm. long, up to 1.2 mm. wide. Petals much smaller than the sepals, elliptic-ovate, acute, 1-nerved, about 0.9–1.2 mm. long and 0.5–0.9 mm. wide. Lip shorter than the petals but broader, orbicular in outline, about 0.8–1.1 mm. in greatest length and equally broad, with a pair of basal, retrorse obliquely triangular-incurved auricles, 3-nerved, rather fleshy. Column minute, yellowish or creamy white.

This species, which has the characteristic appearance of the genus, appears to be most closely allied to the Colombian *Lepanthopsis acuminata* Ames, but is a larger plant, with less acuminate sepals, dissimilar lip and differently colored flowers.

Venezuela: Bolivar [Mount], Ptari-tepuí, at 1600–2000 meters altitude, epiphytic, occasional in the southwest slope forest, flowers deep wine-color with yellowish column, December 17, 1952, *Bassett Maguire & John J. Wurdack 33866* (Type in Herb. Ames No. 68943). Bolivar, El Dorado road, 22 km. south of camp km. 88, "sepals and petals bright purple with smooth-glandular surface." *G. C. K. Dunsterville 425* (Herb. Garay No. 6956).

BOTANICAL MUSEUM LEAFLETS
HARVARD UNIVERSITY

CAMBRIDGE, MASSACHUSETTS, APRIL 4, 1958 VOL. 18, NO. 4

PLANTAE AUSTRO-AMERICANAE X
AMERICAE AUSTRALIS PLANTAE NOVAE VEL ALIA RATIONE SIGNIFICANTES

BY

RICHARD EVANS SCHULTES

ONE hundred years ago, Richard Spruce predicted that the northwestern parts of the Amazon Valley, especially that part lying in Colombia, would be found to be an area peculiarly rich in plants still unknown to science. Continued studies of collections made from this region during the past ten or fifteen years convince us of the soundness and wisdom of Spruce's observation.

The present paper, a miscellany of notes treating chiefly of new species and varieties, furthers a series directed towards our understanding of the flora of South America, with primary reference to the northwestern Amazonia.

It is with appreciation that I acknowledge the collaboration of the following specialists: Dr. John Wurdack (*Melastomaceae*) and Dr. Bassett Maguire (*Guttiferae*) of the New York Botanical Garden; Dr. José Cuatrecasas (*Paraprotium*) and Dr. Richard S. Cowan (*Calliandra, Cassia, Inga, Jacqueshuberia, Macrolobium*) of the Smithsonian Institution; Dr. John D. Dwyer (*Tachigalia*) of St. Louis University; Dr. Harold N. Moldenke (*Eriocaulon*) of the Trailside Museum; and Dr. Robert Woodson (*Apocynaceae*) of the Missouri Botanical Garden. I likewise thank Miss Ruth Barton for the careful

line drawings which she has prepared of several of the novelties. These drawings and their publication were made possible through a grant from the National Science Foundation.

The families are arranged in accordance with the Engler-Gilg system, and the genera are enumerated alphabetically under the families.

Cycadaceae

Zamia madida *R. E. Schultes sp. nov.*

Truncus grandis, elongato-obovoideus, valde amylaceus, 10–18 cm. longus, basi 5 7 cm. in diametro, perfecte subterraneus, apice multis bracteis fibroso-coriaceis, siccis, fuscis, elongato-triangularibus, usque ad 6 cm. longis et basi 0.5–1 cm. latis coronatus. Folia una ad tres, cum petiolo usque ad sex ped. longa; petiolo robusto, valde sulcato, basi rigidissimo sed apicem versus aliquid flexuoso, basi spinulis lignosis brevibus armato, basi 1 -1.5 cm. in diametro; rhachide 1.3–1.5 m. longa; segmentis leviter coriaceis, supra nitida, infra pallidiora, utrinque duodecim ad quattuordecim, oppositis vel subo oppositis, plusminusve 2.5 cm. distantibus, ellipticis vel elliptico-lanceolatis sed vulgo obliquuis, margine leviter revolutis atque basim versus integris sed apicem versus remote et irregulariter dentato-serratis, apice oblique acuminatis, basi in petiolulo plerumque 2–2.5 (sed saepe usque ad 5) cm. longo productis et laminarum base ipsa collo conspicuo coronatis, plerumque 30–40 cm. longis, 5–7 cm. latis, nervis numerosis, parallelis, plusminusve triginti quattuor. Strobilus femineus inter foliis solitarius, in pedunculo erecto, robusto, subterete, apicem versus valde carnoso-inflato, stramineo, dense sed minute lanato, usque ad 30 cm. longo, 1–1.5 cm. in diameter, cylindricus, apice apiculatus, 7–8 cm. longus, densissime brunneo-tomentellus, peltis in seriebus plusminusve sex

verticalibus, hexagonis, majoribus 8–9 mm. longis, 5–6 mm. latis; semina non visa. Strobilus masculus parvus, in pedunculo gracillimo debileque, plusminusve 15 cm. longo, 9–10 mm. in diametro, densissime brunneo-tomentellus, peltis in seriebus plusminusve octo, 4 mm. longis, 2 mm. latis.

Zamia madida is so named (Latin for "drenched") in allusion to the extraordinarily humid forest habitat which it prefers. The forests of the Golfo de Urabá area of northwestern Colombia have one of the heaviest rainfalls in all tropical America, receiving between five and six yards of rain a year. The plant is not uncommon in the region of Mutatá, but it does not occur in colonies, as do many other species of *Zamia*. It is a majestic plant, sometimes as tall as a man, and grows erect, not sprawling, with the heavy ends of the leaves, on which the large leaflets are borne, slightly flexuous.

Zamia madida is well characterized by the very conspicuous swelling at the base of the leaflets. This swelling forms a strong collar which almost completely surrounds the apical part of the petiolule.

COLOMBIA: Departamento de Antioquia, Municipio de Mutatá, Villa Arteaga. Altitude about 150 feet. "In forest." February 16–20, 1953. *Richard Evans Schultes & Isidoro Cabrera 18694* (TYPE in Herb. Gray).—Same locality and date. *Schultes & Cabrera 18640*. (TYPE of male inflorescence in Herb. Gray).—Same locality and date. *Schultes & Cabrera 18679*.

ARACEAE

Anthurium apaporanum *R. E. Schultes sp. nov.*

Caudex abbreviatus, circiter 1.5 cm. in diametro. Petiolus robustior, crassus, canaliculatus, geniculo brevi instructus, usque ad plusminusve 30 cm. longus, 6 mm. in diametro. Folia firme chartacea, pallide viridia, late lanceolata, apice breviter acuminata, basi cuneata, usque ad 40 cm. longa, 12 cm. lata, nervis lateralibus primariis

EXPLANATION OF THE ILLUSTRATION

PLATE XVIII. *ZAMIA MADIDA R. E. Schultes.* 1, habit sketch. 2, portion of leaf, about two fifths natural size. 3, pistillate inflorescence, about two fifths natural size. 4, basal portion of leaflet, showing collar. 5, segment of staminate inflorescence, about two and one half times natural size. 6, staminate inflorescence, about two fifths natural size.

Drawn by RUTH BARTON

Plate XVIII

EXPLANATION OF THE ILLUSTRATION

PLATE XIX. ANTHURIUM APAPORANUM *R. E. Schultes.* Habit, slightly less than one quarter natural size; and fertilized pistillate flower, slightly less than five times natural size.

Drawn by RUTH BARTON

Plate XIX

ANTHURIUM
apaporanum
R. E. Schultes

B

angulo 60° a costa abeuntibus, inter se 8–12 mm. distantibus et in nervum collectivum medio a margine 2–3 mm. remotum. Pedunculus ad 42 cm. longus, 8 mm. in diametro. Spatha lanceolata, 8 cm. longa, 1.5 cm. lata, apice acutiuscula, viridis. Spadix viridis, sessilis, usque ad 16 cm. longis, 15 17 mm. in diametro. Tepala omnino albido-pulverulenta, circiter 2 mm. lata, 4 mm. longa. Pistillum rufum, ovoideum, 4 mm. longum, 3 mm. in diametro.

Anthurium apaporanum appears to be nearest to the complex of *A. Harrisii* (Grah.) Endl., but several differences in floral structure and in relative size of the vegetative parts would suggest that the two concepts are best considered as distinct. In many of its vegetative characters, *Anthurium apaporanum* likewise resembles *A. napaeum* Engl., but the two are easily separated by floral differences.

Colombia: Comisaría del Vaupés, Río Kananarí, Cerro Isibukurí. On sandstone cliffs. "Spadix and spathe green." August 4, 1951. *Richard Evans Schultes & Isidoro Cabrera 13335* (Type in Herb. Gray).

Anthurium nanum *R. E. Schultes sp. nov.*

Herba epiphytica. Caudiculus crassus, internodiis abbreviatis. Folia subcoriacea, petioli strictissimis, crassis, teretibusque, sulcatis, usque ad 2.5 3.5 cm. longis, 0.5 mm. in diametro, lamina pallide viridis, glabra lineari-lanceolata, apice acuminata, basi longe cuneata, margine inconspicue et leviter revolta, 6.5–7 cm. longa, 8–10 mm. lata, nervis crassioribus, utrinque prominentibus. Spatha membranacea, triangularis, apice crasso-apiculata, utrinque albido-pulverulenta, rosea, 9 mm. longa, basi 3–3.5 mm. lata, vivo reflexa. Spadix sessilis, cylindricus, apice truncatus, 11–12 mm. longus, plusminusve 2 mm. in diametro, rufo-purpureus.

It would appear that *Anthurium nanum*, set apart be-

cause of its small stature, as its name implies, is allied to the complex of *A. gracile* (Rudge) Engl. and to *A. fontoides* R. E. Schultes. The type specimen, while a fully mature individual, is of note because of its very diminutive size.

COLOMBIA: Comisaría del Vaupés, Río Kananarí, Cachivera Palito. Altitude about 250 m. "Epiphyte. Spathe pink. Spadix red." July 25, 1951. *Richard Evans Schultes & Isidoro Cabrera 13183* (TYPE in Herb. Gray).

Philodendron colombianum *R. E. Schultes sp. nov.*

Herba in locis humidis crescens, usque ad 1½ pedes alta. Folia ovata, apice sensim cuspidato-acuminata, basi cordata, usque ad 20 cm. longa, 10 cm. lata, nervis lateralibus angulo circiter 30° a costa adscendentibus, marginem versus conjunctis; petiolus apicem versus callosus, plusminusve 18 cm. longus, teres, inferne vagina obtectus. Pedunculus basi in bracteis fibrosis inclusus, plusminusve 9 cm. longus, 2 mm. in diametro. Spatha apice subacuta, intus alba sed extus purpurascens, 5 cm. longa, 3.5 cm. lata, tubus ventricosus fauce valde contractus, 3.5 cm. longus, 1–1.5 cm. in diametro. Spadix stipitate, 5–6 mm. longo suffultus, usque ad 6 cm. longus. Inflorescentiae pars feminea 2.5 cm. longa, plusminusve 11 mm. in diametro, pars mascula 2.4 cm. longa. Stamina 1 mm. longa, 1.2 mm. lata. Pistillum 1–1.2 mm. longum, 0.3 mm. in diametro. Ovarium quattuor- vel quinqueloculare.

COLOMBIA: Comisarías del Amazonas y Vaupés, Río Apaporis, Soratama (above mouth of Río Kananarí) and vicinity. Altitude about 900 feet. March 26, 1952. *Richard Evans Schultes & Isidoro Cabrera 16087* (TYPE in Herb. Gray).

Stenospermatium verecundum *R. E. Schultes sp. nov.*

Suffrutex parvus, in savannarum arena crescens. Cau-

dex valde abbreviatus, circiter 2 cm. crassus. Folia membranacea, atroviridia irregulariter albido-maculata, lanceolato-linguiformia, utrinque glabra, apice acutissima cum apiculo flexuoso, 13–17 mm. longo, basi inaequaliter rotundata, in petiolo 5–9 cm. longo, basi purpureo- et roseo-maculato, ad vaginam latiusculo, 7–30 mm. longo producta; lamina 11–15 cm. longa, 2.5–4 cm. lata; nervis lateralibus angulo acuto adscendentibus. Pedunculus crassus, usque ad 20–22 cm. longus sed vulgo brevior, in vagina foliacea saepe inclusus, apicem versus, 2 mm. in diametro. Spatha aperta lanceolato-elliptica, longe acuminata, usque ad 9 cm. longa, 1.5–1.8 cm. lata, utrinque viridia. Spadix cylindricus, apicem versus tenuior, stipitate robusto, brevi, minute albo-granuloso, 4 mm. longo, 4–5 mm. in diametro suffultus. Staminum filamenta late linearia, 0.5 mm. longa, antherae minutissimae. Pistilla 1 mm. longa, vertice tetragono stigmate coronata.

The long and flexuous apicules on the leaves of this new species seem to set it apart from other concepts of *Stenospermatium*. *Stenospermatium verecundum* would appear to be nearest to *S. Ulei*, at least vegetatively, but the former has a much shorter and stouter peduncle than the latter species.

Stenospermatium verecundum is apparently endemic to the quartzitic mountains of Amazonian Colombia, where it grows in white sandy savannahs, under conditions of extreme xerophytism. It is often associated in the field with the lichen *Cladonia*, as illustrated in the accompanying photograph (Plate XXII).

The specific name, meaning "modest," refers to its inconspicuous habit of growth.

COLOMBIA: Comisarías del Amazonas y Vaupés, Río Piraparaná, Cerro E-ree-eé-kö-mee-ö-kee. "Terrestrial. On sterile sand. Spathe green on both sides, spadix white. Leaves green on both sides. Base of stem mottled purple-brown and pink." September 18, 1952. *Richard Evans Schultes & Isidoro Cabrera 17496* (TYPE in Herb. Gray).

Urospatha somnolenta *R. E. Schultes sp. nov.*

Herba paludosa saxicola, usque ad 2.5–3 pedes alta. Rhizoma spongiosum. Folia erecta, papyracea, hastato-sagittata, latiloba, supra atroviridia, infra vix pallidiora, utrinque glabra, nervis utrinque prominentibus; lobo antico lanceoloto-triangulari, apice acuminato, usque ad 25 cm. longo, parte inferna 10 cm. lato; lobis lateralibus paullo longioribus, oblongo-lanceolatis, sinu profunde parabolico distantibus, costis posticis in sinu 2 cm. denudatis, nervis lateralibus primariis lobi antici duo superioribus angulo acuto adscendentibus in apice exeuntibus, infimo juxta margine fere totius lobi procurrente, nervis loborum lateralium superioribus adscendentibus marginem versus conjunctis. Petiolus apicem versus callosus, parte callosa geniculata, plusminusve 3 cm. longa, usque ad 85–90 cm. longus, aliquid turgido-carnosus, atroviridis et conspicue purpureo-maculatus. Pedunculus robustior, turgido-carnosus, colore petiolo similis, usque ad 55–60 cm. longus, basi 1 cm. in diametro. Spatha anguste lanceolata, longe acuminata, statu juvenili valde spiraliter contorta adulta apicem versus contorta, extus atropurpurea vel nigro-purpurea, intus atroviridis, 15–18 cm. longa, basi 3 cm. lata. Spadix purpureus, apparenter non stipitatus, usque ad 5–6 cm. longus, 3–3.5 cm. in diametro, maturitate valde reflexus. Flores usualiter quinque-tepali, purpurei. Ovarium obovoideum, vulgo biloculare. Bacca obovoidea, 6–7 mm. longo, 4.5 mm. crassa. Semina subreniformia, laeviter rufo-punctulata.

Urospatha somnolenta resembles *U. sagittifolia* (Rodach.) Schott, *U. Sprucеana* Schott and *U. decipiens* Schott, both of which occur in the northwest Amazon.

Urospatha somnolenta appears to be a more robust plant than is generally reported for *U. sagittifolia* and its varieties. It is rather outstanding in its choice of habitat—sandy and boggy holes and crevasses in rocks in the vicin-

ity of waterfalls. It is likewise noteworthy in the strongly drooping position which the ripening fruiting head gradually assumes. The very young spadix stands perfectly erect, but, as the fertilized ovaries enlarge, the spadix bends and finally droops in a deeply nodding position, as shown in the accompanying habit photographs. I have not seen this peculiarity reported for the other species of *Urospatha*; none of the herbarium specimens which I have studied give indication of it, nor have I observed it in any other species of the genus which I met in the field. The specific epithet *somnolenta* (Latin meaning "full of sleep") refers to this apparently unusual nodding position of the mature spadix.

COLOMBIA: Comisarías del Amazonas y Vaupés, Río Apaporis, Raudal Yayacopi (La Playa) and vicinity. Altitude about 800 feet. "In damp crevasses in rocks, in sand and stagnant water. Stem mottled green-purple. Spathe dark green inside, dark purple-black outside. Fruit dark purple-green." February 16, 1952. *Richard Evans Schultes & Isidoro Cabrera 15402* (TYPE in Herb. Gray).

ERIOCAULACEAE

Eriocaulon vaupesense *Moldenke sp. nov.*

Herba parva annua; foliis caespitosis tenuiter membranaceis fragilibus graminodeis 3.5–5.5 cm. longis fenestratis glabris; pedunculis 7–14 cm. longis solitariis gracillimis stramineis tricostatis; vaginis arcte adpressis 2–2.5 cm. longis glabris; capitulis parvis hemisphaericis albis 3–5 mm. latis; bracteolis late obovatis crassis stramineis imbricatis nitidis ca. 1.6 mm. longis ad apicem rotundatis.

Small, probably annual, herb; stem much abbreviated or obsolete; leaves tufted, very thin-membranous and fragile, apparently erect when fresh, spreading or reflexed in age, linear and grass-like, uniformly pale-green on both surfaces, 3.5–5.5 cm. long, 1.5–2 mm. wide below the middle, attenuate-subulate at the apex, fenestrate, gla-

brous on both surfaces; peduncles usually one per plant, 7–14 cm. long, very slender, stramineous, 3-costate, glabrous; sheath slender, closely appressed, 2–2.5 cm. long, glabrous throughout, split at the apex, the blade about 5 mm. long, erect or the tip very slightly spreading, subulate-tipped, glabrous; heads small, hemispheric, white, 3–5 mm. wide; involucral bractlets broadly obovate, thick-textured, stramineous, closely appressed and imbricate, about 1.6 mm. long and wide, shiny, rounded at the apex, glabrous; receptacular bractlets similar but appressed, white-pilose on the back and shortly white-barbate towards and at the apex with stiffly erect hairs; staminate florets: sepals 3, connate at the base, cuneate-spathulate, about 0.8 mm. long and 0.4 mm. wide, rounded and white-barbate at the apex with stiffly erect hairs; petals 3, connate into a slender stramineous tube about 0.8 mm. long, the free tips densely white-barbate like the sepals; stamens 6; filaments very short, about 0.16 mm. long, glabrous; anthers oblong, dark-brown, about 0.2 mm. long and 0.12 mm. wide; pistillate florets not seen.

Since the type locality of *Eriocaulon vaupesense* lies on the boundary between Colombia and Venezuela, this species probably occurs also in Venezuela.

COLOMBIA: Comisaría del Vaupés, Río Guainía, Caño del Caribe (between Isla del Venado and San José) and vicinity. Altitude 850–900 feet. Lat. 2°45′ N, Long. 67°50′ W. November 2, 1952. *Richard Evans Schultes, Richard E. D. Baker & Isidoro Cabrera 18274* (TYPE in U.S. Nat. Herb.).

ARISTOLOCHIACEAE

Aristolochia georgica *R. E. Schultes sp. nov.*

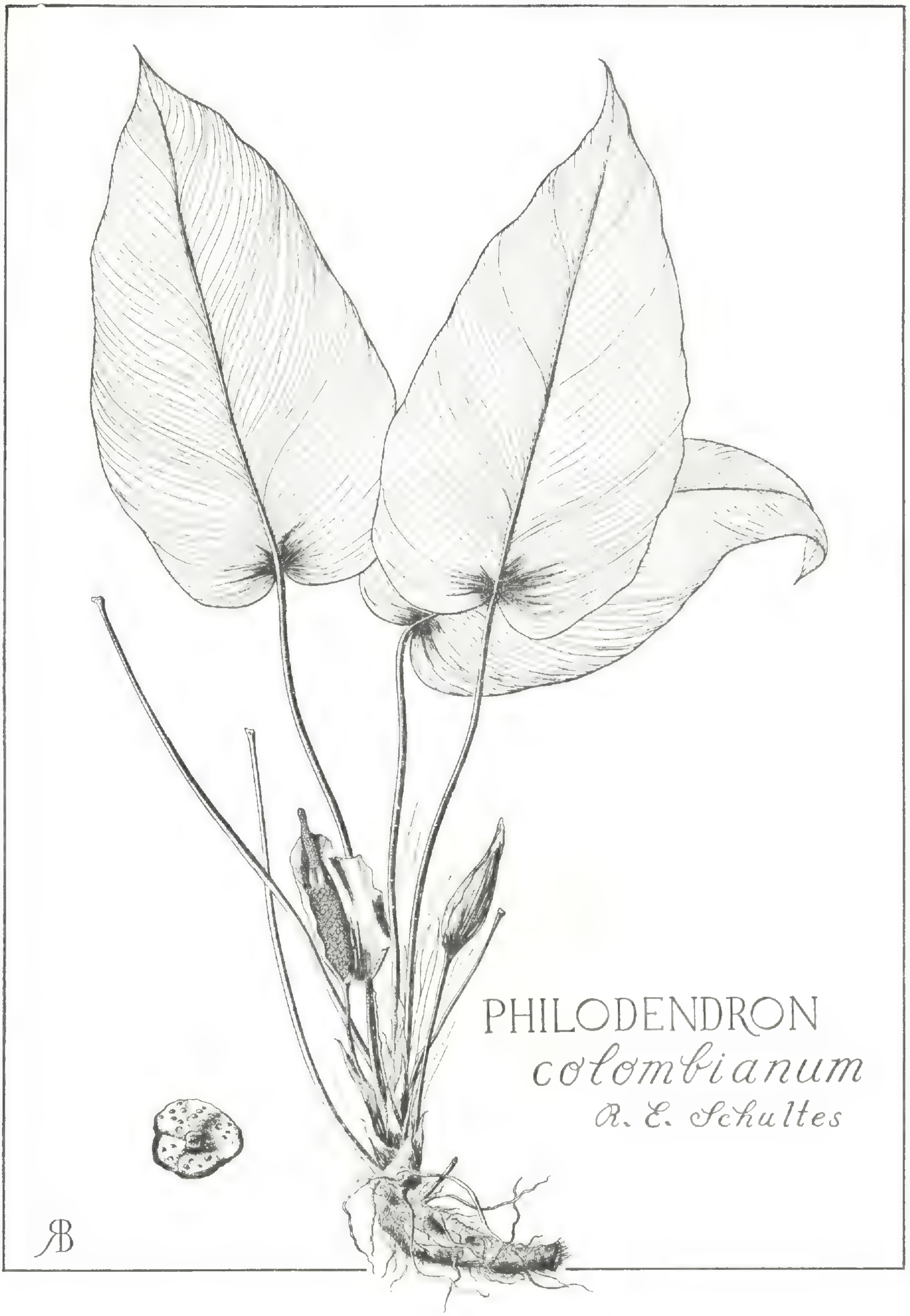
Frutex scandens, gracilis. Caulis volubilis; rami volubilis, teretes, striolati, cum cortice fusco-brunneo, tenui, minutissime puberulente. Folia exstipulata, coriacea vel firme chartacea, oblonga, apice breviter apiculata, basi

EXPLANATION OF THE ILLUSTRATION

PLATE XX. PHILODENDRON COLOMBIANUM *R. E. Schultes.* Habit, approximately two fifths natural size; and fertilized pistillate flower, approximately nine times natural size.

Drawn by RUTH BARTON

Plate XX



PHILODENDRON
colombianum
R. E. Schultes

RB

EXPLANATION OF THE ILLUSTRATION

PLATE XXI. STENOSPERMATIUM VERECUNDUM *R. E. Schultes*. 1, habit, approximately one third natural size. 2, inflorescence, approximately two thirds natural size.

Drawn by RUTH BARTON

PLATE XXI

EXPLANATION OF THE ILLUSTRATION

PLATE XXII. STENOSPERMATIUM VERECUNDUM *R. E. Schultes*. Habit photograph of the colony from which the type collection was made.

Photograph by RICHARD EVANS SCHULTES

Plate XXII

EXPLANATION OF THE ILLUSTRATION

PLATE XXIII. UROSPATHA SOMNOLENTA *R. E. Schultes*. 1, leaf, approximately one sixth natural size. 2, ripening spadix with spathe, approximately one sixth natural size. 3, position of fully ripened spadix. 4, fertilized pistillate flower, approximately three and one half times natural size.

Drawn by RUTH BARTON

PLATE XXIII

EXPLANATION OF THE ILLUSTRATION

PLATE XXIV. UROSPATHA SOMNOLENTA *R. E. Schultes.* Habit photograph of the colony from which the type collection was made.

Photograph by RICHARD EVANS SCHULTES

Plate XXIV

EXPLANATION OF THE ILLUSTRATION

PLATE XXV. UROSPATHA SOMNOLENTA *R. E. Schultes.*
Ripening spadix of the type plant.

Photograph by RICHARD EVANS SCHULTES

Plate XXV

valde contorta, petiolata (petiolo plusminusve 1.5–2 cm. longo, pulverulenta-puberulente), nervis lateralibus plerumque quattuor, supra vivo atroviridia, siccitate straminea, nitidissima, nervis non conspicue elevatis, glaberrima, subtus vivo pallide viridia, nervis omnibus prominenter elevatis, minutissime albido-tomentulosa, cum petiolo usque ad 12–14 cm. longa, plerumque plusminusve 4 cm. lata. Flores in racemis congestis, multifloribus et axillaribus, plusminusve 5.5 cm. longis, pedunculo minutissime pulverulento, gracile, usque ad 3 3.5 cm. longo. Perianthii pars inferna valde ovoideo-dilatata, usque ad 20 mm. longa, 5 mm. in diametro, extus minutissime pulverulens, intus carnoso-verrucosus; tubus cylindricus, 8 12 mm. longus, plusminusve 2 mm. in diametro, apicem versus saepe paullo dilatatus; limbus altero latere expansus, altero truncatus, membranaceus, intus distanter hirtellus, brunneo-viridis, extus minutissime pulverulentus, brunneo-purpureus, oblongus, apice rotundatus et saepe minute apiculatus, apiculo dense aureo-tomentoso, usque ad 22 mm. longus, 10 mm. latus. Columna genitalis 3 mm. longa, breviter stipitata, per dimidium sex-divisa; lobis pseudo-stylinis acutis. Stamina sex in serie unica, columnae adnata, antheris linearibus, usque ad 0.8 mm. longis, longitudinaliter dehiscentibus. Fructus late ellipsoideus, usque ad 8 cm. longus, 3.5 cm. in diametro, pedunculo usque ad 2.5 cm. longo. Semina cuneato-subquadrata, fusco-cinerea, plusminusve 10 mm. lata, 7 mm. longa, altero latere aliquid nitida, altero dense papillosa.

Aristolochia georgica, so named because it prospers most successfully in disturbed agricultural plots near human habitation, belongs to Hoehne's section *Exstipulatae*. It does not appear to resemble closely any species hitherto described. Vegetatively, it suggests *Aristolochia cornuta* Mast. of Amazonian Brazil and Peru, but there

are many major floral differences to separate the two concepts. It also looks vegetatively rather like *Aristolochia iquitensis* O. C. Schmidt, but the lip of the flower is very different.

Of interest as a peculiarity of *Aristolochia georgica* is the curious dense, golden, tomentose apicule terminating the broad, oblong, rounded lip. The species is unusual in the *Exstipulatae* in having a many-flowered inflorescence.

Colombia: Comisarias del Amazonas y Vaupés, Río Apaporis, Soratama (between Río Kananari and Río Pacoa). Altitude about 250 m. "Vine. Flowers mottled green and brownish purple. Puinave name =*too-cheé-ka-pee*. On flood-bank." August 27, 1951. *Richard Evans Schultes & Isidoro Cabrera 13737* (Type in Herb. Gray).

Aristolochia xerophytica *R. E. Schultes sp. nov.*

Suffrutex scandens, in locis arenosis maxime calidis crescens. Caulis volubilis; rami volubiles, teretes, substriolati, cum cortice fusco-brunneo, tenui, minutissime puberulente. Pseudostipulae foliis similes sed multo parviores, usque ad 1.5 cm. longae. Folia exstipulata, coriacea vel firme chartacea, oblongo-cordata, basi cordiforme incisa, apice subacuta, petiolata (petiolo 1–3 cm. longo, pulverulento-puberulente), nervis lateralibus plerumque duo, supra apparenter atroviridia, minutissime et irregulariter scrobiculata, nervis non conspicue elevatis, subtus pallide viridia vel cinereo-viridia, minute et dense hirsuta, cum petiolo usque ad 8–9 cm. longa, parte mediana 1.5–3 cm. lata. Flores apparenter semper solitari; pedunculo gracile, pulverulento, usque ad 3 cm. longo. Perianthii pars inferna valde subglobosa vel ovoideo-dilatata, 0.7–10 mm. in diametro, extus fusca, glabra, intus aliquid verrucosa; tubus cylindricus, 9–10 mm. longa, 4 mm. in diametro, apicem versus valde infundibuliformis; limbus altero latere valdissime expansus, altero truncatus, membranaceus, intus subglabrus sed apicem versus albido-hirsutissimus, apparenter flavo-

EXPLANATION OF THE ILLUSTRATION

PLATE XXVI. ARISTOLOCHIA GEORGICA *R. E. Schultes.* Flowering and fruiting branch, approximately one half natural size.

Drawn by RUTH BARTON

PLATE XXVI

brunneus, extus subglabrus, lanceolatus, apicem versus paullo dilatatus, apice ipso abrupte et breviter acuminatus, usque ad 32 mm. longus, basi 10 mm. latus. Columna genitalis 2.5–3 mm. longa, non stipitata, apice sex-divisa; lobis pseudostylinis obtusis, 0.7 mm. longis. Stamina sex in serie unica, columnae valde adnata, antheris linearibus, plerumque 2 mm. longis, longitudinaliter dehiscentibus. Fructus adhuc ignotus.

Aristolochia xerophytica does not seem to match closely any of the species included in Hoehne's *Pseudostipulosae*. Except for its foliaceous stipules, it would seem vegetatively to resemble most closely *Aristolochia rumicifolia* Mart. & Zucc., but the flowers of the two species are very dissimilar.

As the specific name implies, *Aristolochia xerophytica* grows in a hot, dry and sandy region, a rather unusual habitat for members of this genus.

Peru: Provincia de Jaen, Departamento de Cajamarca. Near Junta on Huancabamba River. "Herbaceous vine, growing in very hot, dry, sandy soil. Flower pelican-shaped, brown." August 3, 1943. *E. L. Ekman 540* (Type in U.S. Nat. Herb. 1953576; 2105024).

Leguminosae

The descriptions and discussions of *Calliandra*, *Cassia*, *Inga*, *Jacqueshuberia* and *Macrolobium* have been contributed by Dr. Richard S. Cowan; of *Tachigalia* by Dr. John Dwyer.

Calliandra vaupesiana *Cowan sp. nov.*

Arbuscula, ramulis albo-pilosulis et brunneo-puberulis; stipulae persistentes, 4–5 mm. longae, 1.5 mm. latae, lanceolatae, acutae, externe minuto-strigulosae, intus glabrae; petioli 5–7 mm. longi, eglandulares, albo-strigulosi vel -puberuli et brunneo-puberuli, rhachibus 13–33 mm. longis, albo-strigulosis vel -puberulis et brunneo-puberulis; pinnae 3–6-jugatae, anguste oblongae, petiolis

secundariis 1 mm. longis, minute albo-strigulosis, rhachibus secondariis 4.5–9 cm. longis, minute albo-strigulosis: foliola sessilia, 56–70-jugata, approximata, anguste oblonga, haud falcata, apice obtusa ad subacuta, basaliter excentrico-rotundata, glabra, margine minute parceque ciliolato, obscure 2–3-nervia infra, supra laevia, pinnarum foliolis mediis, 7–12 mm. longis, 1–1.5 mm. latis; inflorescentiae axillares in axillis foliorum superiorum et terminales, capitatae, pedunculo 18–22 mm. longo, minute albo-striguloso, floribus sessilibus, rubris, perianthio externe albo-sericeo (corolla densissime sericea), intus glabro; calyx cupularis, tubo ca. 3.5 mm. longo, lobis 0.6–1 mm. longis, ovatis, acutis; corolla infundibuliformis, tubo ca. 5 mm. longo, lobis ovatis, 3 mm. longis, 2 mm. latis, acutis; filamenta 5 cm. longa, glabra; ovarium densissime sericeum, stylo glabro; fructus 90 mm. longus, 12 mm. latus, oblongus, ad basim angustior, velutinus.

The specific epithet, derived from the name of the geographic region from which these four collections were taken, seems appropriate in light of the apparent restricted distribution of many species of *Calliandra*.

The new species does not seem to have any very close relatives; it may be recognized by the large number of small, subglabrous leaflets, the few pairs of pinnae, and the rather large, sericeous flowers.

Colombia: Comisaría del Vaupés, Río Kuduyarí, Cerro Yapobodá. Sabanas sobre piedras areniscas. Altitude about 450 m. October 3–4, 1951. *Richard Evans Schultes & Isidoro Cabrera 14203* (Type in U.S. Nat. Herb. 2171380).—Comisaría del Vaupés, Río Paraná Pichuña. Altitude about 700 ft. June 1953. *Schultes & Cabrera 19915*.—Comisaría del Vaupés, Río Karurú, Mesa de Yambí, Savannah de Gooran-hoo-dá. Altitude 950–1000 ft. April 1953. *Schultes & Cabrera 19152*.—Comisaría del Vaupés, Río Kuduyarí, Yapobodá. Quartzite savannah near headwaters. Altitude 900–1000 ft. April 1953. *Schultes & Cabrera 19985*.

EXPLANATION OF THE ILLUSTRATION

PLATE XXVII. ARISTOLOCHIA XEROPHYTICA *R. E. Schultes.* Flowering branch, approximately one half natural size.

Drawn by RUTH BARTON

Plate XXVII

Cassia gigantifolia (*Britt. & Killip*) *Cowan comb. nov.*

Chamaefistula gigantifolia Britton & Killip, N. Y. Acad. Sci. 35 (1936) 171.

This collection has been compared with the type (*G. Klug 1622*) at the New York Botanical Garden, and there is little doubt of their conspecificity, although the petals of the *Schultes* collection are larger; those on the type are up to 2 cm. long, and those in the present collection are up to 3.5 cm. long.

COLOMBIA: Comisaría del Vaupés, Río Negro, San Felipe and vicinity. *Richard Evans Schultes, Richard E. D. Baker & Isidoro Cabrera 17964.*

Inga involucrata *Cowan sp. nov.*

Arbuscula, ramulis juvenilibus strigosis sed mox glabrescentibus; stipulae persistentes, subcoriaceae, 15–23 mm. longae, 10–12 mm. latae, ovatae, acuminatae, glabrae; folia glabra, 3-jugata, petiolo 47 mm. longo, alis oblongis, 41 mm. longis, 6 mm. latis, glandula disciformi, sessili, 3.5 mm. diametro, rhache 18 cm. longa, alis oblanceolatis, 75–85 mm. longis, 6 mm. latis; foliola subcoriacea, discolora, elliptica, base obtusa ad subobtusa, apice acuta, faciebus ambobus costa salienti sed infra validiore, venis primariis 10-15 costae utroque latere, supra leviter impressis, infra valde salientibus, venulis obscuris, foliolorum jugo inferiore 16.5 cm. longo, 7.5 cm. lato, jugis superioribus ca. 25–30 cm. longis, 9.5–12 cm. latis; inflorescentiae axillares, capitatae, pedunculo 7.5–9 cm. longo, sparse strigoso, glabrescenti, floribus subsessilibus, viridibus, involucratis (bracteis imbricatis, multis, sparse strigosis ad glabris subtendentibus), bracteis exterioribus ovatis, acutis, 7–10 mm. longis, 6.5–8.5 mm. latis, bracteis interioribus ellipticis, acutis, ca. 8–10 mm. longis, 5 mm. latis, pedicellis 1.5 mm. longis, strigosis; calycorum tubus glaber, ecostatus, subcylindricus,

sparse strigosus, 21–23 mm. longus, apice 8–9 mm. diametro, calycorum dentibus triangularibus, 3 mm. longis, strigosis; corolla immatura, apice strigosa; gynoecium glabrum.

Inga involucrata is not closely related to any other known species. It is abundantly distinct by virtue of its persistent, foliaceous stipules and bracts; the latter form a conspicuous involucre (hence the specific epithet) at the apex of the peduncle, subtending the subsessile flowers. Another very striking feature of the new species is the very large calyx; the only species which shares this character is *Inga inflata* Ducke, an Amazonian species, but this probably does not indicate very close relationship, for in all other respects the two species are quite dissimilar.

Colombia: Departamento de Antioquia, Golfo de Urabá, Municipio de Mutatá, Villa Arteaga. Altitude about 150 ft. February 16–20, 1953. *Richard Evans Schultes & Isidoro Cabrera 18651* (Type in U.S. Nat. Herb. 2172228).

Inga longifoliola *Cowan sp. nov.*

Arbuscula vel arbor ad 3 m. alta, ramulis minute strigulosis, albo-lenticellatis; stipulae caducae, ca. 2.5 mm. longae, 0.7 mm. latae, acutae, anguste ellipticae; folia parce minuto-strigulosa, petiolis teretibus, 20–22 mm. longis, rhachibus 24–33 mm. longis, teretibus ad marginatis, glandulis sessilibus et ca. 2 mm. diametro; foliola 2-jugata, raro unijugata, petiolulis 2–2.5 mm. longis, laminis 13–17.5 cm. longis, 3–5 cm. latis, anguste ellipticis ad lanceolato-ellipticis, base acutis, apice longo-acuminatis, faciebus ambobus parce strigulosis, supra metallicis et nitidis, costa salienti, venis primariis ca. 15-jugatis, supra planis, infra salientibus; inflorescentiae axillares, pedunculo (30–) 45–55 (–62) mm. longo, minute striguloso, axe ca. 12–15 mm. longo, minute striguloso, bracteis caducis, lanceolatis, acutis, 2 mm. longis et 1 mm. latis, externe minute strigulosis, intus glabris,

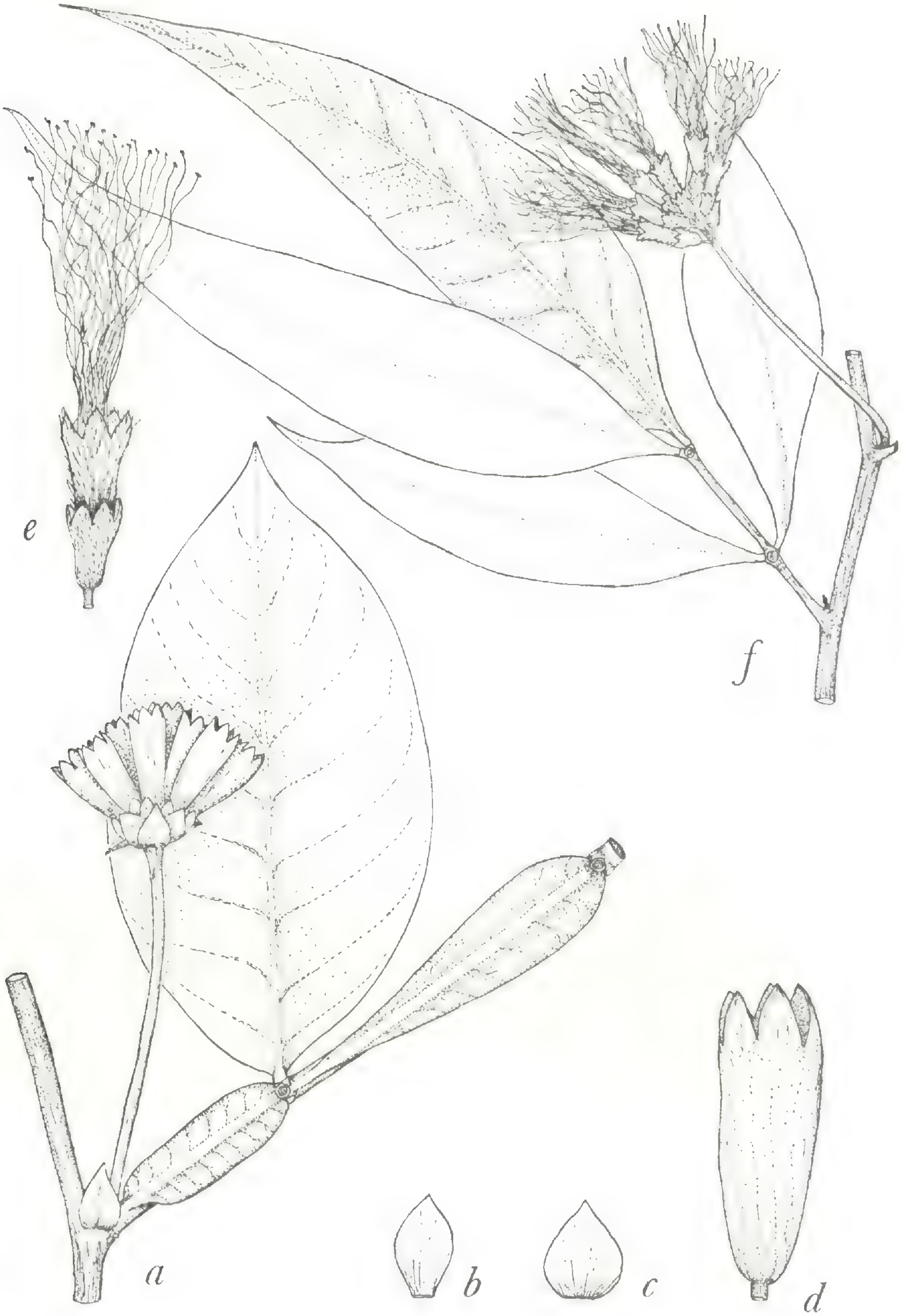
EXPLANATION OF THE ILLUSTRATION

PLATE XXVIII. a–d, INGA INVOLUCRATA *Cowan*. a, habit, one half natural size. b, calyx, one and one half times natural size. c, outer bract of inflorescence, one and one half times natural size. d, inner bract, one and one half times natural size.

e–f, INGA LONGIFOLIOLA *Cowan*. e, habit, one half natural size. f, one flower, one and one half times natural size.

Drawn by RICHARD S. COWAN

Plate XXVIII



pedicellis 1.5–2 mm. longis, minute strigulosis: calyx brevi-cylindricus, 7–9 mm. longus, strigulosus, tubo 5–6 mm. longo, lobis triangularibus, 2–3.5 mm. longis, acutis; corolla villoso-sericea, 14–18 mm. longa, tubo 11–14 mm. longo, ad apicem dilatato, lobis lanceolatis ad ovatis, acutis, 3–4 mm. longis; filamenta ca. 35–40 mm. longa, tubo 15–20 mm. longo, incluso vel parce exserto: gynoecium glabrum.

The long, narrow leaflets of the new species provide the basis for the specific epithet. It is probably not closely related to *Inga strigillosa*, but it has many characters in common with this species. Both have terete petioles and rhachis (terete to marginate rhachis in the new species), the leaflets of both are in two pairs and they have a metallic lustre on the upper surface, the pubescence is alike, and the inflorescence is very similar. The two species differ in the size of all the flower parts and the width-length ratio and the shape of the leaflets.

Colombia: Comisaría del Vaupés, Río Apaporis, Jinogojé (at mouth of Río Piraparaná) and vicinity. "Bush. Flowers white." September 25, 1952. *Richard Evans Schultes & Isidoro Cabrera 17609* (Type in U.S. Nat. Herb. 2172944).—Same locality. June 1952. *Schultes & Cabrera 16677*.—Same locality. July 1952. *Schultes & Cabrera 19807*.—Comisaría del Amazonas, Río Caquetá, La Pedrera and vicinity. May 1952, *Schultes & Cabrera 16382*.

Jacqueshuberia amplifoliola *Cowan sp. nov.*

Arbor probabiliter, ramulis juvenilibus parce strigulosis; petioli 3.5–5 cm. longi, parce strigulosi, rhachibus 5–7 cm. longis, marginato-canaliculatis, parce strigulosis; pinnae 3-jugatae, petiolis secundariis 10 mm. longis, rhachillibus 5.5–8 cm. longis, marginato-canaliculatis, parce strigulosis; foliola glabra, coriacea, supra nitida, 6–8-jugata, sessilia, 18–28 mm. longa, 8–15 mm. lata, oblonga, base inaequilateralia et acuta, apice rotundata retusaque, costa plana, venulis obscuris; inflorescentiae

terminales, composito-racemosae, ca. 35–40 cm. longae, parce strigulosa, bracteis deciduis, lanceolatis, acuminatis, 3.5 mm. longis; pedicelli 17–20 mm. longi, graciles, parce strigulosi, hypanthio 4–4.5 mm. longo, cupulare; sepala 5, externe strigulosa, ciliolata, duo late triangularia, 3.5–4 mm. longa, 4.5 mm. lata, cetera sepala ovalia, 5–5.5 mm. longa, 4–4.5 mm. lata, apice rotundata; petala 5, ovalia, ciliolata, externe ad basem parce strigulosa, intus glabra, 6.5–7 mm. longa, 4.5 mm. lata; filamenta ca. 30 mm. longa, base villosa, tubo inaequale 10 mm. longo cohaerenti, antheris oblongis, 5.5–6 mm. longis, mucro 0.5 mm. longo praedito; stigma capitellatum, stylo glabro, ca. 10 mm. longo, gracili; ovarium ad marginem sparse strigulosum vel glabrum, lateraliter profunde unisulcatum.

There certainly is no difficulty in distinguishing this species from the two previously described ones. Those have very numerous, small leaflets and *Jacqueshuberia amplifoliola* (as the epithet implies) has relatively very large and fewer leaflets; there are also abundant floral characteristics to separate the species. The nearest relative of the new one is *Jacqueshuberia quinquangulata* which has pubescent ovaries, deeply sulcate branchlets, etc., in addition to the very different leaves.

COLOMBIA: Comisaría del Vaupés, Río Kubiyú, Cerro Kañendá. Savannah about 15 miles upstream from mouth. Quartzite base. Altitude about 800–900 ft. November 10, 1952, *Richard Evans Schultes & Isidoro Cabrera 18402* (TYPE in U.S. Nat. Herb. 2195820).—Same locality and date. *Schultes & Cabrera 18376.*

Macrolobium microcalyx *Ducke* var. **minimum** *Cowan var. nov.*

A var. *microcalyce* ramulis puberulis, foliis 2–3-jugatis, rachibus 7–17 mm. longis, canaliculatis, foliolis ad basim inaequilateralibus, latere superiore acuto, latere inferiore obtuso, infra glaucis, bracteolis glabris intus, extus pu-

berulis, 2 sepalis adaxialibus saepe ad apicem cohaerentibus, petalarum lamina glabra, ovario marginaliter villoso differt.

The differences separating this variety from the typical one are not strikingly obvious, but they are sufficiently important to justify recognition. The epithet is intended to convey the impression that the new variety is a smaller form of *Macrolobium microcalyx*. The leaflets of this new variety are mostly in two or three pairs, and most of the leaflets are smaller than those characteristic of the typical variety. The under surfaces of the leaflets are glaucous, the bracteoles are glabrous on the inner surface and the ovary is marginally villose instead of completely villose as in the typical variety.

COLOMBIA: Comisaría del Vaupés, Río Kananarí, Cerro Isibukurí. Piedra de arenisca. Altitude 250–700 m. October 28, 1951. *Richard Evans Schultes & Isidoro Cabrera 14456* (TYPE in N.Y. Bot. Gard.).

Tachigalia Schultesiana *Dwyer sp. nov.*

Arbores magnae; virgae teretes minute velutinae; stipulae non visae; folia ad 20 cm. longa; petioli graciles, 0.2–0.4 cm. lati, dense pubescentes vix canaliculati myrmecodomatio oblongo, ad 4 cm. longo, ad 1.5 cm. lato, saepe infra primum foliolorum jugum constructo; rhachides graciles ad 0.15 cm. lati, dense pubescentes; petioluli dense pubescentes ad 0.3 cm. longi; foliola 8–10-jugata, tenui-coriacea minute puberula supra dense velutina infra (praecipue in costa venisque) inaequilateraliter angusto-oblonga, 2.5–8 cm. longa, 1–2.3 cm. lata, apice obtusa ultime distincte acuminata, costa prominula venis principalibus 6–10 supra prominulis subevanescentibus infra subprominentibus subrigidis arcuato-ascendentibus, marginibus revolutis; inflorescentiae dense velutinae, racemis ad 18 cm. longis rhachidibus circ. 0.2 cm. in medio latis, inferioribus evidenter arcuato-ascendentibus

superioribus laxioribus et gradatim brevioribus, floribus multis mox deciduis; bracteolae mox deciduae lanceolatae, ad 6 mm. longae, ad 2 mm. latae; pedicelli ad 1.5 mm. longi; calyx receptaculi inaequilateraliter cupuliformis pariete circ. 0.35 mm. crasso extus dense pubescente: sepala tenui-carnosa oblonga vel ovata-oblonga, ad 4 mm. longa, 3–3.2 mm. lata, utrinque dense lanulosa comis paucis parvis rubescentibus corporibus mistis, marginibus villosulis; petala in vivo lutea oblonga, 4–5 mm. longa, basi unguiculata villosa intus praeter margines (extus comis paucis basi) venis evidentibus; filamenta subulata, 4–7.5 mm. longa, 0.3–0.35 mm. basi lata, villosa basi comis solum intus dispositis, antheris circ. 1.3 mm. longis; stipes ovarii 1.3–2.7 mm. longus, aureo-villosus, ovario ad 3 mm. longo, circ. 1.5 mm. lato, dense aureo-villoso stylo ad 4 mm. longo, ovulis 6–8; fructus non visi.

Tachigalia Schultesiana, named in honor of one of the collectors of the type material, is marked by multijugate leaves. Only two other species of the genus, *Tachigalia polyphylla* Poepp. & Endl. and *T. multijuga* Benth., have numerous pairs of leaflets. The smaller flowers of the new species, with uniformly thick filaments of the stamens, suggest immediately a close relationship with *Tachigalia polyphylla* of Amazonian Brazil.

A number of floral characters distinguish *Tachigalia Schultesiana* from *T. polyphylla:* the receptacle-cup is cupuliform in outline rather than oblong-rotund, the hairs of the petals are subappresed, fewer, and do not extend to the margins, the anthers are longer, the stipe of the pistil is thicker and much longer at maturity, and the ovarian hairs are frequently fewer along the two longitudinal areas of the valves, thus giving the ovary a striate appearance.

Occasional petals show small and scattered glandular

EXPLANATION OF THE ILLUSTRATION

PLATE XXIX. a–c, JACQUESHUBERIA AMPLIFOLIOLA *Cowan*. a, habit, one half natural size. b, one flower, one and one half times natural size. c, portion of inflorescence, one half natural size.

d–f, CALLIANDRA VAUPESIANA *Cowan*. d, habit, one half natural size. e, two leaflets, illustrating variation in size and shape, three times natural size. f, one flower, one and one half times natural size.

Drawn by RICHARD S. COWAN

Plate XXIX

bodies among the hairs. These have been observed previously in petals of *Tachigalia*, although occurring on the inner surface of sepals of several species.

Apparently individual flowers or small clusters of flowers are subjected to insect attack. Gall-like formations, somewhat rounded and measuring up to 1.5 cm. length, result. The pedicel of a gall-bearing flower is obvious; the receptacle-cup, while tumescent and abnormally large, maintains much of its symmetry, and the sepals and petals are larger, more crassate, and apparently more pubescent. The stamens and pistil form an amorphous mass within. Dissection of the mass reveals that it is somewhat coriaceous in texture: pollen grains and ovules were not found. These gall-like structures are soon deciduous.

COLOMBIA: Comisarías del Amazonas y Vaupés, Rio Apaporis, Cachivera de Jirijirimo and vicinity. Altitude about 250 m. "Large tree. Flowers yellow." September 16, 1951. *Richard Evans Schultes & Isidoro Cabrera 14045* (TYPE in Herb. Mo. Bot. Gard.).

BURSERACEAE

Paraprotium amazonicum *Cuatrecasas sp. nov.*

Arbor magna, ramis extremis minute tomentulosis brunneis angulosis. Folia alterna composita, in specimine paripinnata 8-juga, 90–100 cm. longa, foliolis petiolulatis oppositis. Petioles 30 cm. longus robustus rigidus striatus basi incrassato-dilatatus, minute puberulus vel glabratus in rhachidem productus. Rhachis 40 cm. longa internodiis 5–6 cm. longis striata minute puberula. Petioluli circa 12 mm. longi robusti erecti vel striati minute puberuli. Lamina foliolorum oblonga, basi rotundata subsymmetrica vel leviter asymmetrica (in foliolis duobus terminalibus basi cuneata asymmetrica excepto), apicem versus paulo attenuata apice subite cuspidato-caudata, margine integerrima, 14–26 cm. longa, 5.5–7 cm. lata,

plus caudicula 2–2.5 cm. longa; supra in sicco pallide brunnescenti nitida glabra costa angusta notata, nervis secundariis filiformibus prominulisque, nervulis minoribus reticulatis plusminusve prominulis; subtus pilis minutis conicis rubellis copiosis praedita, costa crassa elevata striata puberula, nervis secundariis 12–16 utroque latere prominentibus patulis prope marginem subite arcuatis anastomosatisque, ceteris nervis laxum reticulum prominulum formantibus. Inflorescentiae axillares, in specimine fructiferae ad terminationem ramuli, paniculatae; axibus robustis striatis, basi valde incrassatis, minute tomentulosis 22–30 cm. longis, ramulis patulis 7– cm. longis tomentellis. Pedicelli fructiferi crassi 2–4 mm. longi tomentosi. Fructus vulgo 1-pyrenus oblique ovatus basi asymmetrice rotundatus extremo acutiusculus in sicco 2.2–2.5 cm. longus, 1.5 cm. latus, vel 2-pyrenus late ovatus adpressus basi subtruncatus apice subacutus in sicco 2.2 cm. altus, 2.3 cm. latus; epicarpio coriaceo extus brunneo tomentoso denique dehiscenti, mesocarpis pulposo, endocarpio corneo. Pyrenus ovoideo-oblongus zygomorphus uno latere gibbosus basi rotundatus apice angustatus triquetro-acutissimus circa 18 mm. longus, 9–10 mm. latus. Epispermum membranaceum, embryone recto cotyledonibus plano-convexis circa 14 mm. longis (in sicco) 6 mm. latis.

Dr. Cuatrecasas writes: "*Paraprotium amazonicum* is closely related to *P. vestitum* Cuatr., from the Pacific Coast of Colombia. It differs from it by its leaves having more numerous oblong, narrower leaflets which are minutely puberulent and more prominently reticulate beneath. Furthermore, *Paraprotium amazonicum* has smaller and more zygomorphous fruits and more acute pyrenes."

Brazil: Estado do Amazonas, Rio Negro, Jucabí (near mouth of Rio Curicuriarí) and vicinity. "Tree 75 feet tall with columnar trunk above buttress and stilt roots to 4 ft. Bark outside smooth, brown,

inside red. Terminal branches with white, latex-like sap. Fruit outside golden, inside smooth, pink. Seed olive green, surrounded by acidic white pulp. On high land." September 21–25, 1947. *Richard Evans Schultes & Francisco López 8835* (TYPE in Gray Herb.).

GUTTIFERAE

Dr. Bassett Maguire has submitted the following critical notes on the genus *Lorostemon*.

In an area near Manáos, where for more than a century the famous botanical explorers of the Amazon Basin (Martius, Spruce, Ule and others) had made headquarters for long periods of time, Ducke discovered a remarkable stand of small trees to which he gave count, ". . . vingtaine d'arbres adultes . . ." From specimens collected there, he described *Lorostemon bombaciflorum* which he proposed (Ducke, A. in Arch. Inst. Biol. Veg. 1 (1935) 210) as the type of a new monotypic subfamily, the *Lorostemonoideae* of the *Guttiferae*. Principal criteria upon which the new subfamily was based were: 1, the arrangement of the anthers, five each in five concrete undivided phalanges; and, 2, the ovary borne on a long gynophore similar to that of many capparids. Arrangement of the stamens in five phalanges is, of course, not unique in the *Guttiferae*, being generally characteristic of the genera of the *Moronobeae*. But the stipitate ovary base was not otherwise known for the family.

I have before me an isotype of *Lorostemon bombaciflorum: Ducke 23768* (NY)—and two additional sheets, *Ducke 944* and *1200*, obtained from the type locality in 1942 and 1943, respectively. All three collections are faithful to the original description.

Now, Schultes and Cabrera have made three additional collections of *Lorostemon*, but from the region of the Río Apaporis, an affluent of the Caquetá or Japurá, some 800 miles to the west and north of Manáos. Two

collections (*Schultes & Cabrera 17619* of September 25, 1952, and *17638* of September 25–26, 1952) differ strongly from the isotype and topotypes of the original species, as the following table of comparison will show. The third, a fruiting collection (*Schultes & Cabrera 15910* of March 2, 1952) has the dark-colored branchlets, smaller gradate and more numerous sepals of *Lorostemon bombaciflorum*, and, as in that species, lacks the conspicuous torus-like peduncle between the bractioles and calyx. The leaves, however, are oblong and not obovate as in *Lorostemon bombaciflorum*. *Schultes & Cabrera 15910* is tentatively assigned to *Lorostemon bombaciflorum* until flowering material of it is collected.

	L. bombaciflorum	*L. colombianum*
Branchlets	dark reddish brown	pale reddish brown
Leaf-blades	10–15×4–6 cm., broadly obovate	18–22×6–7 cm., oblong-elliptic
Calyx	sepals gradate, 9–11, ovate, acute, 6–12 mm. long	sepals little or not at all gradate, 5, orbicular, 18–20 mm. long
Peduncle	peduncles lacking, flowers sessile	peduncle 8–12 mm. long, crassate, turbinate
Petals	80–105×10 mm.	80–90×20 mm.
Stamens	in 5 wholly concrete phalanges, anthers 5 per phalange	in 5 phalanges, filaments adnate only below the middle, above the middle free, anthers 10–12 per phalange, free

Lorostemon colombianum *Maguire sp. nov.*

Arbor mediocris 6–7 metralis alta cum latice luteo; ramulis glabris non-angulatis, tenuis, internodiis 3–6 cm. longis; foliis oppositis aliquando suboppositis vel alternatis; laminis firme chartaceis vel subcoriaceis, oblongis vel elliptico-oblongis, vulgo 18–22 cm. longis, 4.5–7 cm. latis, apice prominente acute et abrupte acuminato, 10

15 mm. longo; basi obtusa vel acuta; costa prominenta, venis lateralibus parallelis, prominulis 1–2 mm. distantibus, nervo collectivo a margine ca. 1 mm. remoto; flora solitari terminale exteriori rubro sursum maculato; bracteis paucis aggregatis acute triangularibus vel ovato-triangularibus 2–5 mm. longis; pedunculo crasso turbinato 5–10 mm. longo; sepalis 5, imbricatis non-gradatis ovato-orbicularibus, 15–18 mm. latis, 15–20 mm. longis, subscariosis; petalis 8–9 cm. longis, ca. 2 cm. latis, lineari-oblanceolatis, apice acutiusculo; staminibus 50–60 in 5 phalangibus, quisque cum 10–12 staminibus; filamentis ad basim ca. 2 cm. in ligulo connatis, partis liberis planis tenuis, ca. 0.6–0.7 mm. latis, 2–2.5 cm. longis; antheris introrsis linearibus 2–2.5 cm. longis, 0.6–0.7 mm. latis, apice saepe recurvato, connectivo aliquantum alato; pistillo longi-stipitato, ovario 5-loculari, ovulis numerosis, stylis brevi-cornutis, 5; fructu ignoto.

Colombia: Comisaría del Amazonas, Río Ricapuyá, tributary of Río Apaporis below mouth of Río Piraparaná. September 25–26, 1952. *Richard Evans Schultes & Isidoro Cabrera 17638* (Type in Herb. N.Y. Bot. Gard.).—Comisarías del Amazonas and Vaupés, Río Apaporis at mouth of Río Piraparaná. "Tree 6 m. high. Flowers red outside, greenish at base and red-spotted above; calyx green. September 25, 1952. *Schultes & Cabrera 17619.*

Melastomaceae

The following studies in the Melastomaceae have been contributed by Dr. John Wurdack.

Centronia vaupesana *Wurdack sp. nov.*

Centroniae reticulatae Triana affinis sed cum foliorum laminis supra non reticulato-venosis indistincte 5-nerviis, ovario apice glabro. Rami robusti indistincte sulcati cum petiolis pedunculoque primum rufo-furfuracei mox glabrati. Petioli 2–3 cm. longi; lamina 11–17×4–7.5 cm. ovata apice hebeti-acuta paulo acuminata) basi rotun-

data, integra 5-nervia nervis duobus exterioribus submarginalibus debilioribus nervis primariis secundariisque supra leviter angusteque impressis subtus bene elevatis nervulis supra obscuris subtus paulo elevato-reticulatis, supra glabra et nitidula, subtus in superficie glabra in nervis sparse furfuraceis. Inflorescentia 4 5 cm. longa pauciflora, floribus 5-meris fasciculatis. Pedicelli 4–7 mm. longi cum hypanthio calyceque setulosi, setis crassis (ad basim 0.3 mm. diam.) usque ad 1.5 mm. longis minute tuberculatis. Hypanthium (ad torum) 7×4–5 mm.; calyx in alabastro clausus 9 mm. longus conicus ad anthesim ad torum dehiscens. Petala 20×18 mm. apice oblique rotundata. Stamina isomorphica; filamenta 6 mm. longa; thecae 7 mm. longae subulatae, connectivo basi non prolongato dorsaliter calcarato calcari acuto 1.6 mm. longo. Stylus ca. 14×0.5 mm.; stigma truncatum; ovarium 5-loculare glabrum apice in collum 1.3 mm. altum circum stylum protractum, collo apice breviter (0.2–0.3 mm.) 10-lobato.

Spruce 4840 (K), the type collection of *Centronia reticulata*, has been compared with *C. vaupesana*. The Peruvian species has striking upper leaf surface venule reticulation, 3-nerved leaf blades with no trace of fourth and fifth veins, slightly larger flowers, and (despite Cogniaux and Triana's 'glabrous' descriptions) the ovary apex sparsely puberulous with slender brown hairs to 0.3 mm. long. *Centronia laurifolia* D. Don is another possible relative, but its leaves are larger and 3-plinerved, the flowers 'subsessile,' and the 'subacute' petals only 1 cm. long.

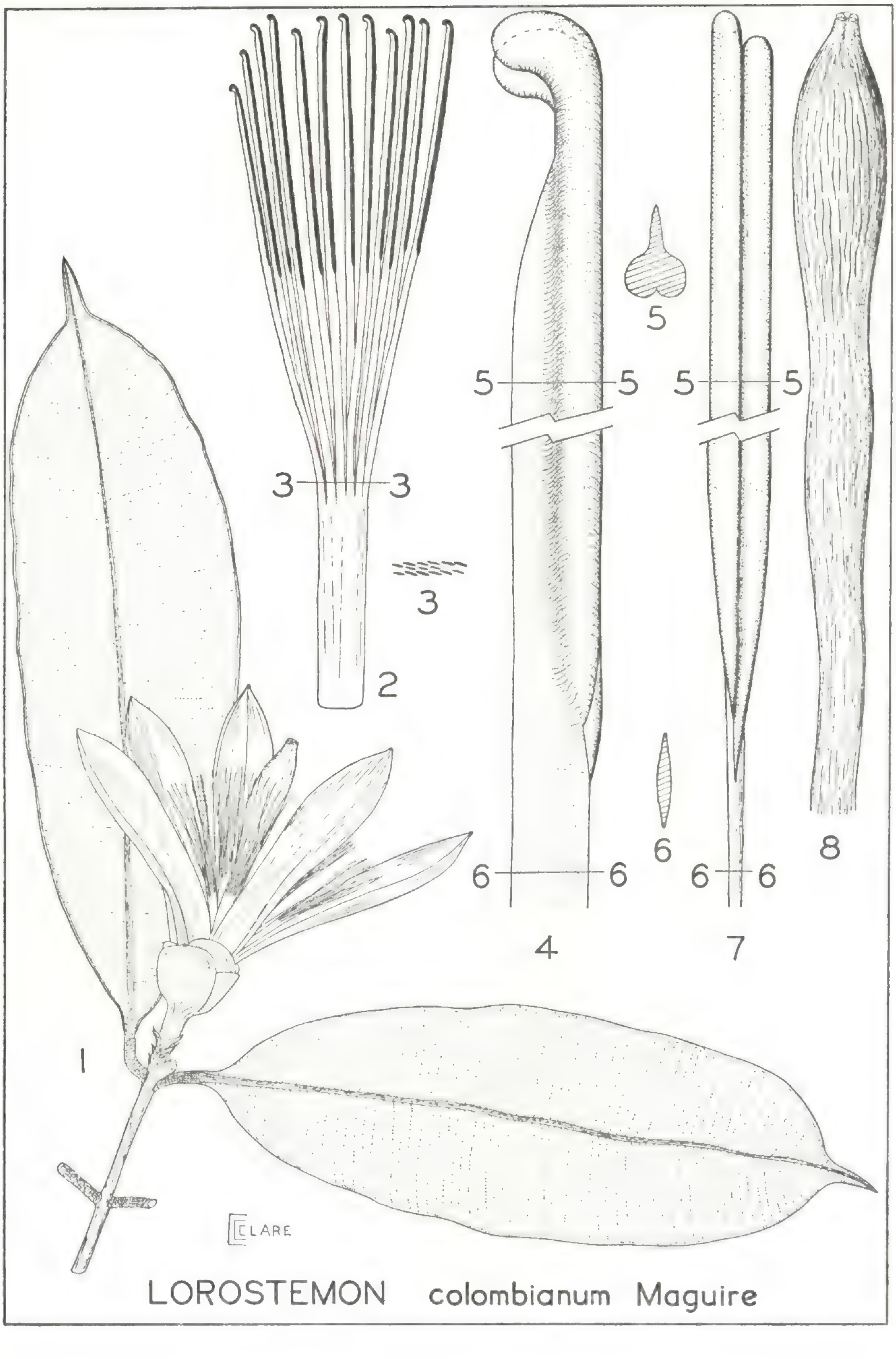
Colombia: Comisaría del Vaupés, Río Piraparaná, Raudal Na-hoógaw-he. "Spindly tree 8 m. tall. Flowers white. Maku name: *kanang*." August 30, 1952. *Richard Evans Schultes & Isidoro Cabrera 17100* (Type in Herb. N.Y. Bot. Gard.).

EXPLANATION OF THE ILLUSTRATION

PLATE XXX. LOROSTEMON COLOMBIANUM *Maguire*, drawn from the holotype, *R. E. Schultes & I. Cabrera 17638* (NY). 1, flowering branch, one half natural size. 2, ventral view of phalange of stamens, one and one half times natural size; note dextrorse orientation of anthers. 3, cross-section diagram showing arrangement and orientation of filaments at position 3-3. 4, ventral view of extrorsely oriented anther, twenty times natural size. 5, cross-section of anther at positions 5-5, twenty times natural size. 6, cross-section of filament at positions 6-6, twenty times natural size. 7, lateral view of anther, twenty times natural size. 8, pistil, one and one half times natural size.

Drawn by C. C. CLARE

Plate XXX



LOROSTEMON colombianum Maguire

Macairea Schultesii *Wurdack sp. nov.*

Macairea arirambae Hub. et *M. scabrae* Cogn. affinis, sed foliis breviter petiolatis 5-nerviis. Fruticosa ca. 1-metralis, ramulis pilis rufidulis eglandulosis appressis ca. 1 mm. longis densiuscule vestitis. Petiolus 2–5 mm. longus; lamina 2.5–6×2–3.5 mm. elliptica vel paulo ovato-elliptica apice late acuta bis obtusa basi obtusa bis subcordata margine integra 5-nervia vel sub 7-nervia, supra dense tuberculato-aspera setis 1 4mm.[2] basi ad 0.4 mm. expansis apice pilo deciduo ad 0.5 mm. longo armatis, subtus densissime strigulosa pilis gracilibus rufescentibus eglandulosis ad 0.3 mm. longis (ad nervos ad 1.5 mm. longis) et cum guttulis flavidis modice interspersa. Bracteae inflorescentiae 3 5×2 3 mm. deciduae sparse pilosulae extus modice gracili-strigulosae et sparse cum guttulis flavidis armatae; pedunculi pedicellique pubescentia ut ramulorum eadem; pedicelli 1 4 mm. longi. Hypanthium 2.7–3×2- 2.3 mm. cum sepalis extus modice graciliterque rufo-strigulosum et cum guttulis flavidis dense inspersum. Sepala ad basim 0.6 0.7 mm. coalita, lobis 1.3–1.8×1.2- 2 mm. triangularibus bis ovatis apice acutis vel obtusis. Petala 7–9×4–6.5 mm. obovata apice rotundata ad marginem apicem versus cum guttulis flavidis armata. Stamina dimorphica, filamentis apicem versus glandulis flavidis brevistipitatis armatis: antherarum thecae apice attenuatae. Stamina maiora: filamenta 7.7–9.3 mm.; antherarum thecae 3.5–5.3 mm., connectivo sub thecis 2 3.2 mm. producto, appendicibus oblongis bis rotundatis 0.7–0.9×0.5–1 mm. Stamina minora: filamenta 4.5–6.5 mm.; antherarum thecae 2.9–4.1 mm., connectivo sub thecis 0.9–1.3 mm. producto, appendicibus oblongis bis rotundatis 0.8 1×0.7 1 mm. Stylus 3.5–4.5 (–10.5)×0.2–0.4 mm. modice cum guttulis flavidis armatus; ovarium 4-loculare totum cum guttulis flavidis apicem versus brevistipitatis (ad 0.1 mm.

modice vel dense armatum; semina 0.7×0.4–0.5 mm. cochleata haud profunde foveolata, cum guttulis rubris.

Macairea arirambae and *M. scabra* both have 3-nerved leaves with longer petioles. Other possible relatives are *Macairea albiflora* Cogn. and *M. theresiae* Cogn., both (ex char.) having much larger, longer-petiolate leaves with attenuate bases. Another collection probably referable to *Macairea Schultesii* is *Gutiérrez & Schultes 656* from the Cerro de Chiribiquete, Río Macaya, Vaupés, Jan. 17, 1944; the specimen of this collection in the Herbarium of the New York Botanical Garden is, however, sterile.

COLOMBIA: Comisaría del Vaupés, Río Kuduyarí, Cerro Yapobodá. Savannahs on quartzite base. Altitude about 450 meters. "Bush 2–3 feet tall. Flowers white." October 2–6, 1951. *Richard Evans Schultes & Isidoro Cabrera 14358* (TYPE in N.Y. Bot. Gard.).—Same locality. "Low bush 1–2 feet high. Flowers white." October 4–6, 1951. *Schultes & Cabrera 14350* (US).—Comisaría del Vaupés, Río Kubiyú (tributary of Río Vaupés), Cerro Kañendá. Savannahs about 15 miles upstream from mouth. Quartzite base. Altitude about 800–900 feet. "Shrub. Height 4 feet." November 10, 1952. *Schultes & Cabrera 18324* (NY).—Comisaría del Vaupés, Río Karurú (tributary of Río Vaupés), Mesa de Yambí. Savannah Goo-ran-hoo-dá. Quartzite base. Altitude about 950–1000 feet. "Bush. Flowers whitish to pink." April 15–16, 1953. *Schultes & Cabrera 19146* (US).—Comisaría del Vaupés, Río Paraná Pichuña (tributary of Río Vaupés). Altitude about 700 feet. "Bush. Flowers yellow." June, 1953. *Schultes & Cabrera 19953* (NY).

Siphanthera vaupesana *Wurdack sp. nov.*

A congeneribus circa *Siphanthera Hostmannii* differt trichomatibus paucissimis eglandulosis. Herba 15–25 cm. alta superne multiramosa; ramuli quadrati glabri setis brevibus paucis nodosis exceptis. Folia anguste obovato-elliptica vel anguste elliptica pauci-serrulata; lamina 4–6 ×1.5–2.5 mm. apice acuta basi attenuata uninervia nervulis secondariis paucis, obscure punctata glabra vel supra primum setis paucis brevibus appressis ornata; petiolus

1 2 mm. longus. Glomeruli bracteati 2–4-flori floribus 4-meris subsessilibus (pedicellis 0.2 mm. longis); bracteae foliosae fere sessiles setoso-serrulatae glabrae. Hypanthium cum calyce glabrum cum glandulis sessilibus caducis ornatum; hypanthium 2–2.6×1 mm.; calycis lobi 1.2 1.3×0.6 mm. acuti. Petala ligulata; lamina 0.7×0.6 mm. ovata acuta non setosa; unguis 0.6×0.2 mm. longus. Stamina oppositipetala; antherae 1 1.1× 0.4 mm. (rostro et connectivo exclusi), rostro 0.25×0.1 mm. minute (0.06 mm.) uniporoso, connectivo sub anthera 0.3 mm. producto indistincte bilobulato parte expansa 0.3 mm. lata; filamenta 2.2 mm. longa; staminodia desunt. Ovarium biloculare; stylus 4.5×0.1–0.15 mm. apicem versus leviter expansus; stigma truncatum; capsulum bivalve; semina ellipsoidea 0.4×0.2 0.25 mm. laxe elongato-areolata.

Siphanthera Hostmannii (synonymous with *S. Tatei* Gleason and *S. capitata* Gleason) and its poorly distinguished relatives (*S. tenera* Pohl, *S. subtilis* Pohl, *S. pratensis* Mgf., *S. ramosissima* Cogn. ex Hoehne, *S. paraensis* Huber) all have varying amounts of gland-tipped trichomes. The descriptions and illustrations of all except *Siphanthera Hostmannii*, *S. paraensis* and *S. ramosissima* omit mention of staminodia. All relatives of *S. vaupesana*, except *S. pratensis* and *S. subtilis*, have wide-pored and essentially erostrate anthers.

Colombia: Comisaría del Vaupés, Río Vaupés, Raudal de Yurupari. On sand or quartzite base. November, 1951. *Richard Evans Schultes & Isidoro Cabrera 19723* (Type in N.Y. Bot. Gard. Duplicate type in U.S. Nat. Herb. No. 2,195,539).

Myrsinaceae

Conomorpha lithophyta *R. E. Schultes sp. nov.*

Arbuscula saxicola parva, usque ad decem ped. alta, pauce ramosa, ramulis junioribus minute albido-tomentellis, mox glabrescentibus, ramis cortice cinereo cum

petiolorum cicatricibus conspicuis obtecto. Folia vivo aliquid reclinata; petiolis fuscis, sulcatis, minutissime tomentellis, 2–3 cm. longis, plusminusve 3 4 mm. in diametro; lamina valdissime coriacea, obovata, conspicue marginata, apice obtusa vel rotundata, statu adulto 9 13 cm. longa, 5 6.5 cm. lata, supra vivo atroviridia (siccitate stramineo-fusca), nitida glabraque, nervis haud conspicuis, subtus pallidiora, apparenter glabra sed per vitream minutissime et remote albido-lepidota, nervo centrale valde elevato. Inflorescentiae strictae, saepe rigide arcuatae, numerosae, foliis breviores, densissime multiflorae, usque ad basim florigerae, axi aliquid crassiusculo, dense et molliter aureo-tomentello. Flores sessiles, patentes, plerumque 4 mm. longi, ore 4–4.5 mm. in diametro, albo-lutei, fragrantissimi. Sepala base connata, lobis triangularibus, acutis, plusminusve 1.8 mm. longis, 1 mm. latis, extus dense aureo-glanduloso-tomentellis, intus minute pulverulentis. Petala media pro parte connata, lobis crassioribus, ovatis, apice obtusis, 4 mm. longis, 1.8–2 mm. latus, extus sed intus densiore albido-glanduloso-papillosis. Stamina petalis breviora; filamentis crassioribus et petala adnatis; antheris recurvis, 0.6 mm. longis. Ovarium lageniforme, 0.7 0.8 mm. in diametro, bene lepidatum, stylo cylindrico, crasso, usque ad 1.5 mm. longo. Fructus adhuc ignotus.

The specific epithet of *Conomorpha lithophyta* ("stone-dwelling plant") refers to the habitat chosen by this small, bushy treelet. The Savannah of Yapobodá has a base of metamorphosed quartzite of probable Cretaceous age. The endemic flora which covers it is highly adapted to xerophytism—a xerophytism due primarily to the lack of soil and consequent mechanical loss of rain-water. *Conomorpha lithophyta* inhabits the most inhospitable parts of the savannah and exhibits a predilection for rock outcroppings (see Plate XXXII, lower figure).

The closest ally of *Conomorpha lithophyta* seems to be *C. magnoliifolia* Mez, a species of British Guiana and Surinam. The former can be distinguished from the latter at once by its very compact and densely many-flowered spikes (in contrast to loosely fewer-flowered racemes). There are also minor floral differences, such as the triangular lobes of the calyx and the lageniform ovary in *Conomorpha lithophyta* (in contrast to ovate lobes and a subglobose ovary in *C. magnoliifolia*).

Like *Conomorpha magnoliifolia* in Surinam, this new species is reported to be employed as a minor fish-poison. The Kubeos living along the uppermost course of the Río Kuduyarí sometimes crush the leaves of *Conomorpha lithophyta* for use in fishing in stagnant lagoons. The Kubeo name of the tree is *dá-pee-ka-hee*, meaning savannah (*dá*) fish-poison (*pee-ka-hee*).

Colombia: Comisaría del Vaupés, Río Kuduyarí, Savannah of Yapobodá. "Tree 10 feet tall. Flowers fragrant, yellow. Inflorescence frequented by bees." September 4, 1956. *Arthur F. Barclay & Richard Evans Schultes 560* (Type in Herb. Gray).—Same locality and date, *Barclay & Schultes 543*.—Same locality and date, *Barclay & Schultes 565*.

Apocynaceae

Dr. Robert Woodson has contributed the descriptions and discussions of the apocynaceous plants which are discussed in the following lines.

Mandevilla annulariifolia *Woodson sp. nov.*

Frutex volubilis; ramis crassis vel crassiusculis juventate minute papillatis mox cortice valde anguloso saturate rubro-vernicoso tectis, ramulis saepe verticillatis. Folia verticillata saepissime quaternata subsessilia linearia 2–5 cm. longa, 1–4 mm. lata, firmiter membranacea glabra nervo medio supra distante glanduligero. Inflorescentia terminalis vel subterminalis pauciflora; pedunculo

vix 1 cm. longo minute puberulo; pedicellis ca. 2 mm. longis minute puberulis; bracteis minute ovatis vix 1 mm. longis. Calycis laciniae ovatae acutae ca. 1.5 mm. longae minute papillatae intus basi squamella profunde lacerata munitae. Corolla infundibuliformis lutea extus minutissime papillata; tubo proprio ca. 2 cm. longo basi ca. 1 mm. diam. paululo gibboso; faucibus tubulo-campanuliformibus ca. 1.7 cm. longis, ostio ca. 0.6 cm. diam.; lobis late dolabriformibus patulis ca. 1.2 cm. longis. Antherae late oblongo-sagittiformes basi rotundate 2-lobae ca. 3.5 mm. longae apice minutissime barbatae caeterumque glabrae. Ovarii carpella vix 1 mm. longa glabra nectario late 5-lobo ovario ca. dimidio aequante; stigmate pentagono-umbraculiformi obscure apiculato ca. 1 mm. longo. Folliculi gracillimi falcati obscure articulati usque 10 cm. longi.

Mandevilla annulariifolia is closely allied, indubitably, to *M. Benthamii* of the Roraima shield of interior Venezuela and Guiana, which are low erect shrubs with somewhat broader and thicker leaves and more elongate inflorescences. The suggestively antediluvian appearance of *Mandevilla annulariifolia* is imparted by the narrow, whorled leaves borne in dense tufts at the ends of the thick, frequently whorled branchlets.

Colombia: Comisaría del Vaupés, Río Apaporis, Cachivera de Jirijirimo y alrededores. Altitude about 250 m. September 16, 1951. *Richard Evans Schultes & Isidoro Cabrera 14013* (Type in Mo. Bot. Gard.).—Río Apaporis, Raudal de Jirijirimo, November 27, 1951. *Schultes & Cabrera 14627*.—Río Apaporis, Raudal de Jirijirimo, below mouth of Río Kananarí, December 8, 1951. *Schultes & Cabrera 13503*. —Comisaría del Vaupés, Río Piraparaná, tributary of Río Apaporis, September 18, 1952. *Schultes & Cabrera 17536*.

Mandevilla cuneifolia *Woodson sp. nov.*

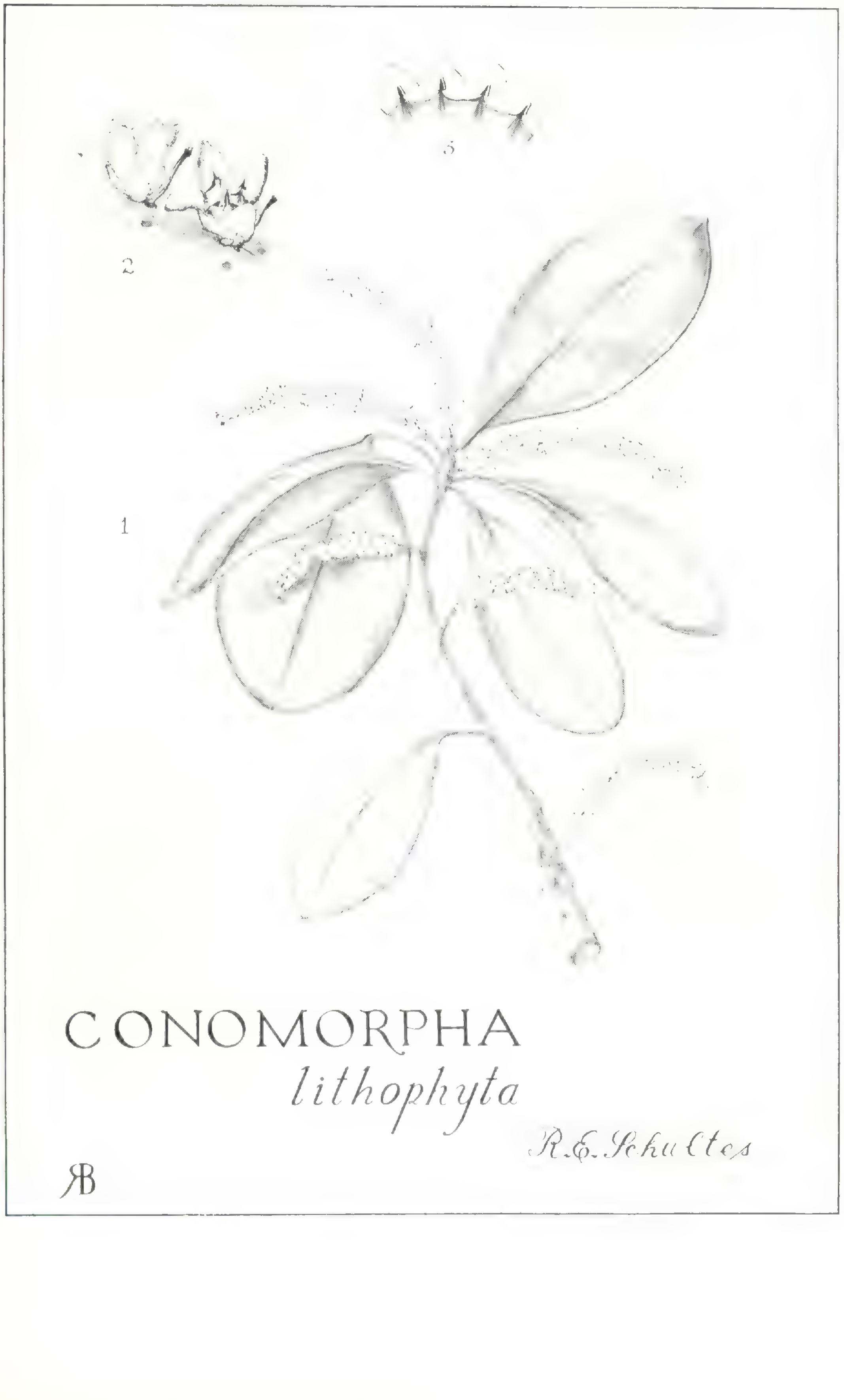
Frutex volubilis; ramulis gracilibus glabris. Folia decussata breviter petiolata; lamina obovata vel elliptico-obovata abrupte acuminata basi acuta 4–7 cm. longa,

EXPLANATION OF THE ILLUSTRATION

PLATE XXXI. CONOMORPHA LITHOPHYTA *R. E. Schultes*. 1, flowering branch, slightly less than one half natural size. 2, portion of inflorescence, showing two flowers, approximately two and one half times natural size. 3, petals opened, approximately twice natural size.

Drawn by RUTH BARTON

Plate XXXI



CONOMORPHA

lithophyta

R. E. Schultes

RB

EXPLANATION OF THE ILLUSTRATION

PLATE XXXII. (*Upper*) View of the quartzitic savannah at Yapobodá, upper Río Kuduyarí, Comisaria del Vaupés, Colombia—type locality of *Conomorpha lithophyta*.

(Courtesy American Orchid Society, Inc.)

(*Lower*) CONOMORPHA LITHOPHYTA *R. E. Schultes*. Flowering branch of the type plant.

Photographs by RICHARD EVANS SCHULTES

Plate XXXII

EXPLANATION OF THE ILLUSTRATION

PLATE XXXIII. CONOMORPHA LITHOPHYTA *R. E. Schultes*. Habit photograph of the type plant.

Photograph by RICHARD EVANS SCHULTES

Plate XXXIII

1.5–2.5 cm. lata firmiter membranacea glabra nervis secondariis arcuatis sat remotis nervo medio supra pauciglanduligero; petiolo 3–5 mm. longo. Inflorescentia lateralis vel subterminalis pauciflora glabra; pedunculo 1–2.5 cm. longo; pedicellis subnullis; bracteis minutissime ovatis. Calycis laciniae ovato-trigonales longe acuminatae extus papillatae intus squamella deltoidea minute erosa munitae. Corolla infundibuliformis lutea extus omnino glabra; tubo proprio 3.5–4 cm. longo basi ca. 1.5 mm. diam.; faucibus conicis ca. 2.5 cm. diam., ostio ca. 1 cm. diam.; lobis late dolabriformibus ca. 2 cm. longis patulis. Antherae obovato-oblongae basi breviuscule auriculatae ca. 3 mm. longae dorso glabrae. Ovarii carpella ovoidea ca. 1.5 mm. longa, nectariis 5 plusminusve connatis subaequilongis; stigmate pentagono-umbraculiformi obscure apiculato ca. 1 mm. longo.

A member of the *Mandevilla scabra* alliance, *M. cuneifolia* is distinguished by the obovate or elliptic-obovate cuneate leaves and reduced inflorescence.

Colombia: Comisaría del Vaupés, Río Piraparaná (tributary of Río Apaporis), Caño Teemeeña, Savannah O-koo-me-gwa, September 6, 1952. *Richard Evans Schultes & Isidoro Cabrera 17234* (Type in Mo. Bot. Gard.).—Comisaría del Vaupés, Río Vaupés, between Mitú and Javareté, Yutica, May 14–24, 1953. *Schultes & Cabrera 19377*.

Mandevilla stephanotidifolia *Woodson sp. nov.*

Frutex volubilis; ramulis teretibus vel paulo compressis glabris. Folia decussata petiolata; lamina latiuscule oblongo-elliptica in acumine breve abrupte contracta basi obtusa vel rotundata 6–12 cm. longa, 4–7 cm. lata subcoriacea subglauca glabra nervo medio supra distante glanduligero; petiolo ca. 1 cm. longo. Inflorescentia aut terminalis aut lateralis spicata multiflora; pedunculo ca. 6–12 cm. longo crassiusculo glabro; pedicellis nullis vel vix bene manifestis; bracteis speciosis petalaceis (albis?) caducis late oblongo-obovatis carinatis apice valde acu-

minatis sessilibus 2.5–3 cm. longis. Calycis laciniae late ovatae acutae ca. 1 mm. longae extus minutissime papillatae intus basi squamella truncate deltoidea praeditae. Corolla infundibuliformis lutea extus glabra vel indistincte papillata tubo laeviter arcuato-gibboso; tubo proprio ca. 3 cm. longo basi ca. 2 mm. diam.; faucibus conicis ca. 1.5 cm. longis, ostio ca. 1 cm. diam.; lobis late dolabriformibus ca. 1.7 cm. longis patulis. Antherae oblongo-ellipticae basi obtuse auriculatae ca. 6.5 mm. longae dorso glabrae. Ovarii carpella gemina oblongo-fusiformia ca. 2 mm. longa indistincte papillata basi nectariis 5 subquadratis carnosis cincta; stigmate pentagono-umbraculiformi longe apiculato ca. 4 mm. longo. Folliculi graciles falcati apice saepe coaliti obscure moniliformes 8–10 cm. longi glabri.

Mandevilla stephanotidifolia is closely related to *M. Steyermarkii* of the Roraima shield, which, however, has slenderer stems, thinner, cordate-ovate leaves, and a slenderer inflorescence.

COLOMBIA: Comisaría del Vaupés, Río Apaporis, Cachivera de Jirijirimo y alrededores. Altitude about 250 m., September 16, 1951. *Richard Evans Schultes & Isidoro Cabrera 14010* (TYPE in Mo. Bot. Gard.).—Río Apaporis, Raudal Jirijirimo, below mouth of Kananarí. Altitude about 900 ft. January 21, 1952. *Schultes & Cabrera 14952.* —Río Apaporis, Raudal de Jirijirimo, November 27, 1951. *Schultes & Cabrera 14632.*—Comisaría del Amazonas, Río Caquetá, La Pedrera and vicinity, May 2, 1952. *Schultes & Cabrera 16325.*

Mandevilla thevetioides *Woodson sp. nov.*

Frutex humilis: ramulis crassis juventate ancipitibus minute puverulo-papillatis mox cortice atrorubescenti tectis. Folia decussata brevissime petiolata lineari-elliptica cum apice tum basi anguste acuta 4–8 cm. longa, 5–10 mm. lata, coriacea margine revoluta venis secundariis multis horizontalibus supra illustria nervo medio pauciglanduligero subtus minutissime velutina; petiolo

ca. 2 mm. longo. Inflorescentia aut terminalis aut subterminalis pauciflora minute puberula; pedunculo crasso 1–2 cm. longo; pedicellis 2–3 mm. longis; bracteis minute ovatis caducis. Calycis laciniae ovatae acutae ca. 2 mm. longae extus puberulo-papillatae. Corolla infundibuliformis alba extus papillata; tubo proprio gracillimo ca. 3 cm. longo basi ca. 1 mm. diam.; faucibus anguste conicis ca. 1.5 cm. longis, ostio ca. 7 mm. diam.; lobis oblique dolabriformibus ca. 2 cm. longis patulis. Antherae late oblongo-sagittatae ca. 4 mm. longae basi obtuse bilobatae dorso glabrae. Ovarii carpella oblongoidea ca. 1.5 mm. longa glabra nectario 5-lobo basi cincta; stigmate pentagono-umbraculiformi obscure apiculato ca. 1.5 mm. longo.

Closely allied to *Mandevilla nerioides*, this new species may be distinguished by the dense horizontal secondary venation of the leaves, minutely velutinous beneath.

Colombia: Comisaría del Vaupés, Río Kananarí (affluent of Río Apaporis), Cerro Isibukuri. October 29, 1951. *Richard Evans Schultes & Isidoro Cabrera 14508* (Type in Mo. Bot. Gard.).

Prestonia vaupesana *Woodson sp. nov.*

Frutex volubilis omnino glaber; ramulis teretibus gracillimis. Folia decussata petiolata; lamina ovato-elliptica acuminata basi obtusa 7–12 cm. longa, 3–6 cm. lata firmiter membranacea; petiolo 5–7 mm. longo. Inflorescentia simplex corymbiformis interpetiolata plurivel multiflora; pedunculo gracile 7–16 cm. longo; pedicellis gracillimis ca. 1.5 cm. longis in fructu accrescentibus; bracteis minimis. Calycis laciniae anguste oblongo-lanceolatae 7–8 mm. longae herbaceae apice saturiorae intus basi squamella truncata munitae. Corolla aut gilva aut livide rosea salverformis; tubo ca. 1.5 cm. longo basi ca. 2.5 mm. diam., annulo conspicuo ca. 1 mm. alto minute papillato, appendicibus epistaminalibus anguste oblongis ca. 2 mm. longis ostio vix attingentibus; lobis

late dolabriformibus ca. 9 mm. longis refractis. Antherae dimidio exsertae lanceolatae ca. 5 mm. longae dorso sparsiuscule pilosulae. Ovarii carpella ca. 1 mm. longa; nectariis carnosis basi connatis ovario aequantibus. Folliculi gracillimi falcati obscure articulati.

The description of new species of *Prestonia* upon suspiciously slight characters and from unicate specimens is a recurring annoyance. Although *Prestonia vaupesana* is very closely related to *P. Lindleyana* Woods., to which it will key out in my revision of the genus (in Ann. Missouri Bot. Gard. 23 (1936) 276), the several collections made by Schultes and Cabrera, all from the same general area in the valley of the Rio Apaporis, give ample evidence of the characters of a natural population. From *Prestonia vaupesana*, *P. Lindleyana* differs in its somewhat more coriaceous, oblong- or obovate-elliptic foliage, in its shorter inflorescence with stouter peduncles and pedicels, and particularly in its rather broadly ovate, more substantial calyx lobes which, with the pedicels, are prominently suffused with purple.

COLOMBIA: Comisaría del Vaupés, Río Apaporis, Cachivera de Jirijirimo y alrededores. Altitude about 250 m. September 16, 1951. *Richard Evans Schultes & Isidoro Cabrera 14039* (TYPE in Mo. Bot. Gard.).—Río Apaporis, Soratama above mouth of Río Kananarí and vicinity. Altitude about 900 ft. January 1952. *Schultes & Cabrera 19611*.—Río Apaporis, Raudal Yayacopi (La Playa) and vicinity. Altitude about 800 ft. August 18, 1952. *Schultes & Cabrera 16974*.—Río Apaporis entre el Río Pacoa y el Río Kananarí. Altitude about 250 m. July 5, 1951. *Schultes & Cabrera 12893*.

Tabernaemontana rimulosa *Woodson sp. nov.*

Fruticulus humilis, ramulis crassiusculis juventate glabris mox cortice tenui griseo-fulvo longitudinaliter exfoliato tectis. Folia decussata subsessilia in paribus aequalibus; lamina anguste oblongo-elliptica apice acuta basi more subpetiolato gradatim decurrente 12–13 cm. longa, 3–3.7 cm. lata coriacea margine leviter revoluta

omnino glabra supra illustria subtus opaca lutescentia reticulo venularum fere omnino immerso. Inflorescentia interpetiolatis subterminalis subsessilis glomerate composita pluriflora; pedunculis pedicellisque perbrevibus; bracteis minimis glabris. Calycis laciniae late ovales apice rotundatae plusminusve inaequales 2.5 3 mm. longae extus glabrae intus supra basim squamellas liguliformes 2 4 gerentes. Corollae albae lobis margine roseo-tingerentibus; tubo cylindrico ca. 1.7 cm. longo, basi ca. 1.5 mm. diam. medio staminigero parte dimidio superiore extus dense minuteque velutino-papillato basim versus glabro; lobis patulis valde oblongo-dolabriformibus ca. 1 cm. longis supra dense minute velutino-papillatis. Antherae sessiles angustissime lanceolatae longe acuminatae ca. 5 mm. longae thecarum parte basali angustissima recta. Ovarii carpella oblongo-fusiformia ca. 1.5 mm. longa glabra basi nectario dimidio longitudine cincta; stigmate late pentagono-umbraculiformi obtuse apiculato ca. 0.7 mm. longo. Fructus ignoti.

This new species is apparently most closely related to *Tabernaemontana coriacea* Link ex R. & S., but it differs significantly in the narrower leaves, the subsessile glomerate inflorescences, the low stature and, particularly, in the thin, loosely exfoliating periderm of the older branches.

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HOW ABSURD CAN A NOMENCLATURAL PROPOSAL BE?

BY

LESLIE A. GARAY AND RICHARD EVANS SCHULTES

BOTANISTS who are interested in plants as living things and not as pretexts for legalistic juggling of nomenclature are becoming increasingly exasperated with the growing amount of attention paid in our congresses and in our journals to hair-splitting and often superficial interpretations of the International Code of Botanical Nomenclature, whose basic reason for existence is precisely to standardize nomenclature and make such quibbling unnecessary. We would be the first to recognize that rules and regulations are essential for the standardization of nomenclature, yet we rebel at the threat that the activity of other taxonomists become more and more subservient to the confusion wrought by those whose only interest in plants seems to be the legalism surrounding the clarification of their proper naming.

TAXON, the journal of the International Association for Plant Taxonomy, has recently been given over largely to articles on nomenclature by individuals and committees. It is with one part of a recent article that we wish to deal in this note, our primary purpose being to point out one of the many absurdities which our congresses are being asked to consider. We refer to the "Report of the Committee for Spermatophyta. Conservation of generic

names I" in Taxon 7 (1958) 184–193. In this report, we find the following proposal for conservation of the name of an orchid genus:

1533. *Bletilla* Reichenb.f. (1851) vs. *Jimensia* (Raf.) (1838) (6–2) (Syn. Prop. Stockholm 223.)

Bletilla has recently been recognized as a distinct genus with some 6 species. Rafinesque's name has never been used. To adopt it would necessitate new combinations.

Even a superficial reading of this proposal is enough to frighten and shock the average botanist into the realization of the lack of seriousness and thoroughness which is unfortunately becoming more common in the work of those whose main interest apparently is to regulate, no matter on how trivial a point, the work of their colleagues who are concerned with the study of plants.

Reichenbach described *Bletilla* in 1853, giving the concept a very appropriate name suggestive of a resemblance to *Bletia;* the same concept, however, had been recognized and adequately treated thirteen years earlier by Rafinesque under the name *Jimensia.* Rafinesque's treatment (Fl. Tellur. 4 (1836) 38) is clear:

909. *Jimensia* R. (Jap. bot.) Petalis ovatis concavis, 2 internis, label. trifido emarg. basi callis 2 obl. medio concavo, col. filif. incurva, stig. bifid. concavo, antheris 2 dorsalis, capsula clavata. Scaposa, fol. gladiatis, fl. spicatis—Type *J. nervosa* R. *Limodorum striatum* Th. fl. jap. scapo angulato, fol. rad. glad. nervosis, fl. cernuis, bracteatis. Japan, fl. yellow. The G. Limodorum contained many anomalies also, sp. with or without spurs, beards or no beards, many kinds of pillars or styles or clinandres &c.

In 1950, before the Stockholm Congress, a Japanese botanist proposed the conservation of *Bletilla.* This proposal was not acted upon in Stockholm. It did not appear in the Paris proposals. Now, the name has been resurrected and proposed for conservation once again, with the most amazing reason: "Rafinesque's name has never been used. To adopt it would necessitate new com-

binations.'' Is it conceivable that a committee of botanists would suggest deviation from the basic rule of priority because an earlier name had not been used or because several new combinations might result? Naturally, most conservative botanists try to resist altering nomenclature in the cases of very large genera or in generic names which have been long or widely used in economic botany or horticulture, but the genus under question is neither large nor of economic or horticultural importance.

Reichenbach's concept included two different entities. He listed two species in the genus, *Bletilla florida* from the New World and *B. gebinae* from the Old World. It is now recognized that *Bletilla florida* belongs in the genus *Bletia*. Rafinesque's concept is concerned only with the true *Bletilla* element, an additional cause for taking up his name for the concept, which would have been obvious if those responsible for this proposal had any knowledge of the plants involved.

In order to forestall absurd and unnecessary legislative action, we herewith make the appropriate transfers to the genus *Jimensia:*

Jimensia formosana (*Hayata*) *Garay & R. E. Schultes comb. nov.*

Bletia formosana Hayata Mat. Fl. Formos. (1911) 323.
Bletilla formosana (Hayata) Schltr. in Fedde Rep. 10 (1911) 256.

Jimensia kotoensis (*Hayata*) *Garay & R. E. Schultes comb. nov.*

Bletia kotoensis Hayata Mat. Fl. Formos. (1911) 325.
Bletilla kotoensis (Hayata) Schltr. in Fedde Rep. 10 (1911) 256.

Jimensia morrisonicola (*Hayata*) *Garay & R. E. Schultes comb. nov.*

Bletia morrisonicola Hayata Mat. Fl. Formos. (1911) 324.
Bletilla morrisonicola (Hayata) Schltr. in Fedde Rep. 10 (1911) 256.

Jimensia ochracea (*Schltr.*) *Garay & R.E.Schultes comb. nov.*

Bletilla ochracea Schltr. in Fedde Rep. 12 (1913) 105.

Jimensia scopulorum (*W.W.Sm.*) *Garay & R.E. Schultes comb. nov.*

Pleione scopulorum W.W.Sm. in Notes R. Bot. Gard. Edinb. (1921) 218.
Bletilla scopulorum (W. W. Sm.) Schltr. in Fedde Rep. 19 (1924) 375.

Jimensia sinensis (*Rolfe*) *Garay & R.E.Schultes comb. nov.*

Arethusa sinensis Rolfe in Journ. Linn. Soc. Bot. 36 (1903) 46.
Bletilla sinensis (Rolfe) Schltr. in Fedde Rep. 10 (1911) 256.
Bletilla chinensis Schltr. Die Orchideen (1914) 107 *sphalm.*

Jimensia striata (*Thunb.*) *Garay & R.E.Schultes comb. nov.*

Limodorum striatum Thunb. Fl. Jap. (1784) 28.
Epidendrum tuberosum Lour. Fl. Cochin. (1790) 523.
Epidendrum striatum (Thunb.) Thunb. in Trans. Linn. Soc. pt. 2 (1790) 327.
Cymbidium striatum (Thunb.) Sw. in Nov. Act. Upsal. 6 (1797) 77.
Cymbidium hyacinthinum Sm. Exot. Bot. 1 (1804) 117.
Gyas humilis Salisb. in Trans. Hort. Soc. 1 (1812) 300.

Bletia hyacinthina (Sm.) R. Br. in Ait. Hort. Kew., ed. 2, 5 (1813) 206.
Jimensia nervosa Raf. Fl. Tellur. 4 (1836) 38.
Bletia gebina Lindl. in Journ. Hort. Soc. 2 (1847) 307.
Bletilla gebinae (Lindl.) Rchb.f. in Fl. Serres, ser. 1, 8 (1853) 246.
Calanthe gebinae (Lindl.) Lodd. ex Rchb.f. in Fl. Serres, ser. 1, 8 (1853) 246.
Bletilla striata (Thunb.) Rchb.f. in Bot. Zeit. 36 (1878) 75.

Jimensia szetschuanica (*Schltr.*) *Garay & R. E. Schultes comb. nov.*
Bletilla szetschuanica Schltr. in Fedde Rep. Beih. 12 (1922) 344.

Jimensia yunnanensis (*Schltr.*) *Garay & R. E. Schultes comb. nov.*
Bletilla yunnanensis Schltr. in Fedde Rep. Beih. 12 (1922) 343.
Bletilla yunnanensis (Schltr.) var. *Limprichtii* Schltr. in Fedde Rep. Beih. 12 (1922) 344.

Excluded Species

Bletilla florida Rchb.f. in Fl. Serres, ser. 1, 8 (1853) 246 = *Bletia florida* R. Br.

Bletilla japonica (A. Gray) Schltr. in Fedde Rep. 10 (1911) 256 = *Arethusa japonica* A. Gray.

STUDIES IN AMERICAN ORCHIDS IV.[1]

BY
LESLIE A. GARAY

IN the following pages, various new species are described and several new combinations of taxonomic importance are proposed, all of which were discovered during routine checking of collections from the Andes. The arrangement of genera follows the phylogenetic system proposed by Rudolf Schlechter in Notizblat des Botanischer Gartens und Museum zu Berlin-Dahlem 9 (1926) 563–591.

Duckeella pauciflora *Garay sp. nov.*

Saxicola, usque ad 50 cm. alta; radicibus satis crassiusculis, leviter puberulis; foliis 2–3 basilaribus, linearilanceolatis, satis coriaceis, 15–30 cm. longis, 3–5 mm. latis; scapo simplici vel in parte superiore pauciramoso, erecto, stricto, 30–50 cm. alto; inflorescentia abbreviata, pauciflora; bracteis navicularibus, lanceolato-triangularibus, ovariis pedicellatis multoties brevioribus, 4–5 mm. longis; floribus satis magnis, succedaneis, flavis; sepalo postico oblongo-obovato, concavo, reflexo, apice acuto, 7-nervio, 20–22 mm. longo, 6–7 mm. lato; sepalis lateralibus leviter obliquis, oblongo-obovatis, concavis, reflexis, 7-nerviis, 20–22 mm. longis, 6–7 mm. latis; petalis valde

[1] Previous numbers of this series were published in the Canadian Journal of Botany, vol. 34 (1956) 241–260, 721–743 and in Bot. Mus. Leafl. Harvard Univ. 18 (1958) 103–108.

tenuis, late ovato-rhombeis, acutis vel obtusis, reflexis, 9-nerviis, 18–21 mm. longis, 8–12 mm. latis; labello complicato, 3-lobo; lobis lateralibus oblongis, obtusis vel subacutis, 3.5–4 mm. longis, lobo intermedio ovato-oblongo, acuto vel obtusiusculo, 14–17 mm. longo, 5–8 mm. lato; disco supra basim multi-cristato, cristis antice in fimbrias dissolutis; columna 8 mm. longa, apice bi-auriculata; ovariis pedicellatis 1.5–2 cm. longis.

This is the second species of the genus to be noted. A third, as yet undescribed, from the Guiana Highlands, is under study at present by Mr. Schweinfurth. *Duckeella pauciflora* differs from *D. Adolfii* Campos Porto & Brade in having a short raceme, larger flowers and differently shaped petals and lip.

Colombia: Comisaría del Vaupés, Río Kubiyú (tributary of Río Vaupés); Cerro Kañendá, savannahs about 15 miles upstream from mouth. Quartzite base. Altitude about 800–900 feet. Nov. 10, 1952. *Richard Evans Schultes & Isidoro Cabrera 18309* (Type in Herb. Ames no. 69675; Duplicate type in U.S. Nat. Herb.); *Schultes & Cabrera 18399* (Herb. Ames no. 69674).—Yapobodá. *P. H. Allen 3203* (U.S. Nat. Herb. no. 1951970).

Sobralia lancea *Garay sp. nov.*

Saxicola, usque ad 50 cm. alta; radicibus fasciculatis, satis crassis pubescentibus; caulibus caespitosis, erectis, parte basali vaginatis, supra paucifoliatis, teretibus, glabris; foliis lanceolatis, apice longe acuminatis, basi in vaginam caulem amplectentem angustatis, subcoriaceis, plicatis, 16–25 cm. longis, 1–1.5 cm. latis; inflorescentia valde abbreviata, bracteis lanceolatis, bifariis, arctissime adpressis omnino obtecta; floribus succedaneis, tenuissimis, glabris; sepalis petalisque inter se simillimis, oblongo-lanceolatis, brevissime acuminatis, 5–7 nerviis, 3 cm. longis, 5 mm. latis; labello ovato-pandurato, basi rotundato, apice undulato; disco a basi usque ad constrictionem bilamellato, lamellis leviter crenulatis, supra dentiformibus, 2.4 cm. longo, supra basim 12 mm., ad

EXPLANATION OF THE ILLUSTRATION

PLATE XXXIV. DUCKEELLA PAUCIFLORA *Garay*. 1, plant, one third natural size. 2, flower, expanded, natural size. 3, lip, twice natural size.

Drawn by RUTH BARTON

Plate XXXIV

apicem 8 mm. lato; columna gracili, alata, 1 cm. longa, falculis nullis; ovariis graciliter pedicellatis, usque ad 2.5 cm. longis.

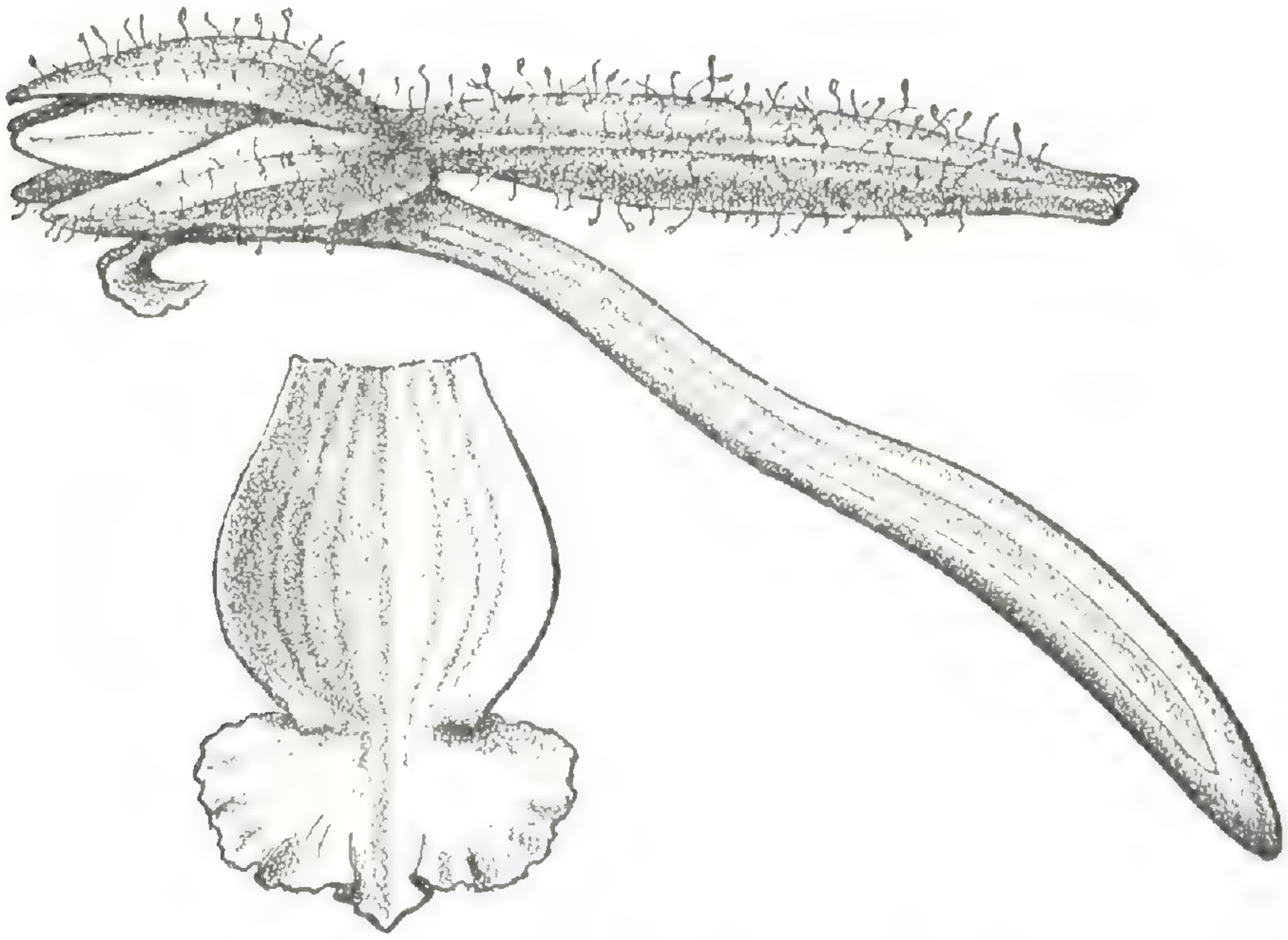
Apparently, the Peruvian *Sobralia candida* (Poepp. & Endl.) Rchb.f. is the only species in the genus with which this new taxon might be confused. Vegetatively these two species are very similar, though *S. lancea* possesses longer and more acuminate leaves. In the floral structures, however, a number of discrepancies can be observed: the sepals and petals are acute in *S. candida* and acuminate in *S. lancea;* in the former the lip is 3-lobed, with the apical lobe wider than the lateral ones; in the latter the lip is pandurate, and the apical portion is much narrower than the basal part. In addition to these differences, *S. candida* is described as having "snow-white" flowers, while the color of *S. lancea* is canary-yellow with purple lamellae on the lip.

COLOMBIA: Auchicayá (Cali-Buenaventura), 500 meters alt. August 11, 1952. *M. Köie 4787* (TYPE in Herb. Ames no. 68437; DUPLICATE TYPE in Herb. Bot. Mus. Univ. Copenhagen).

Erythrodes cylindrostachys *Garay sp. nov.*

Terrestris, usque ad 30 cm. alta; rhizomate longe repenti, satis carnoso, crasso; radicibus crassiusculis, leviter flexuosis, puberulis, albidis; caulibus suberectis vel ascendentibus, primum remote vaginatis, deinde 3–5-foliatis, glabris; foliis ovato-lanceolatis, acuminatis, basi in petiolum attenuatis, mox in vaginam caulem amplectentem dilatatis, 14–20 cm. longis, 2–4.5 cm. latis; inflorescentia cum pedunculo ca. 2 cm. longo densissime puberula, valde compacta, cylindracea, 9–13 cm. longa; bracteis lanceolatis, acuminatis, ovariis brevioribus, 1.6 cm. longis; floribus satis magnis, albidis; sepalo postico ovato-lanceolato, acuto, concavo, 3-nervio, intus glabro, extus sparse glanduloso-hirsuto, 1.2 cm. longo, 4 mm. lato; sepalis lateralibus reflexis, leviter obliquis, ovato-

lanceolatis, 3-nerviis, intus glabris, extus glanduloso-hirsutis, 1.2 cm. longis, 4 mm. latis; petalis ovato-spathulatis, apice acutis vel obtusis, uninerviis, intus extusque glabris, cum sepalo postico galeam formantibus, 1.2 cm. longis, 3 mm. latis; labello trilobo, lobis lateralibus quadratis, antice obtusis, lobo intermedio recurvo, quadrato-reniformi, brevissime apiculato, margine



ERYTHRODES CYLINDROSTACHYS *Garay*

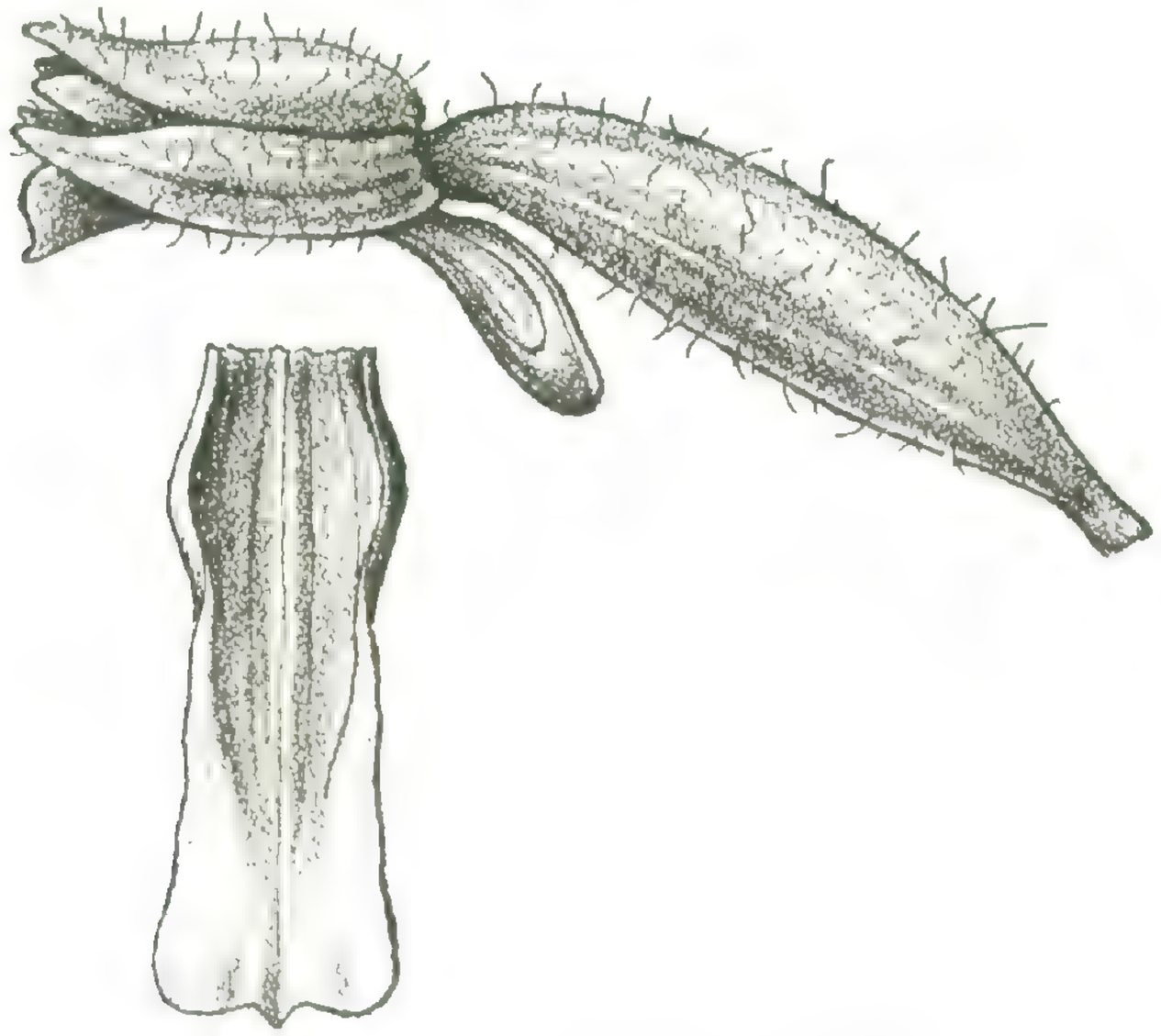
valde undulato, 9 mm. longo, antice 7 mm. lato; calcare cylindrico, leviter sinuato, acuto, 3 cm. longo; ovario cylindrico, glanduloso-hirsuto, 2.2 cm. longo.

This new species has no close alliance among the known taxa. The shape of the lip, together with the long and thick spur, is very different from that in any concept yet described.

COLOMBIA: Departamento del Valle, Cordillera Occidental, vertiente occidental; monte La Guarida, filo de la cordillera sobre La Carbonera (entre Las Brisas y Albán). 1950–2000 meters alt. Oct. 16, 1946. *J. Cuatrecasas 22232* (TYPE in Herb. Ames).—La Cumbre. 1800–2100 meters alt. May 14, 1922. *F. W. Pennell & E. P. Killip 5769* (U.S. Nat. Herb. no. 1141933; Herb. Ames no. 47353).

Erythrodes quadrata *Garay sp. nov.*

Terrestris, usque ad 50 cm. alta; radicibus satis crassis, villosulis; caulibus leviter ascendentibus vel erectis, dimidio inferiori 5 6-foliatis, supra remote vaginatis; foliis erecto-patentibus, petiolatis; lamina ovata vel ovato-lanceolata, acuta, basi abrupte vel sensim in petiolum angustata, 7–10 cm. longa, 2.5 4 cm. lata; racemo



Erythrodes quadrata *Garay*

cylindrico, satis dense multifloro, ca. 8 cm. longo; bracteis lanceolatis, acuminatis, ovariis aequilongis seu paulo brevioribus; floribus in genere inter minores; sepalo postico ovato, obtuso, uninervio, concavo, intus glabro, extus sparse piloso, 3 mm. longo, 1.5 mm. lato; sepalis lateralibus falcato-oblongis, acutis vel obtusis, uninerviis, intus glabris, extus sparse pilosis, 3.5 mm. longis, 1.5 mm. latis; petalis cum sepalo postico galeam formantibus, obovatis, acutis, vel obtusis, basim versus attenuatis, glabris, 3 mm. longis, 0.75 mm. latis; labello quadrato-oblongo, basi valde concavo, supra medium utrinque plicato, antice truncato et in medio brevissime apiculato, 3 mm. longo, antice 1.5 mm. lato; disco a basi usque ad

plicam unicarinato; calcare porrecto, clavato, 2 mm. longo, 1 mm. crasso, ovario tertia parte breviore.

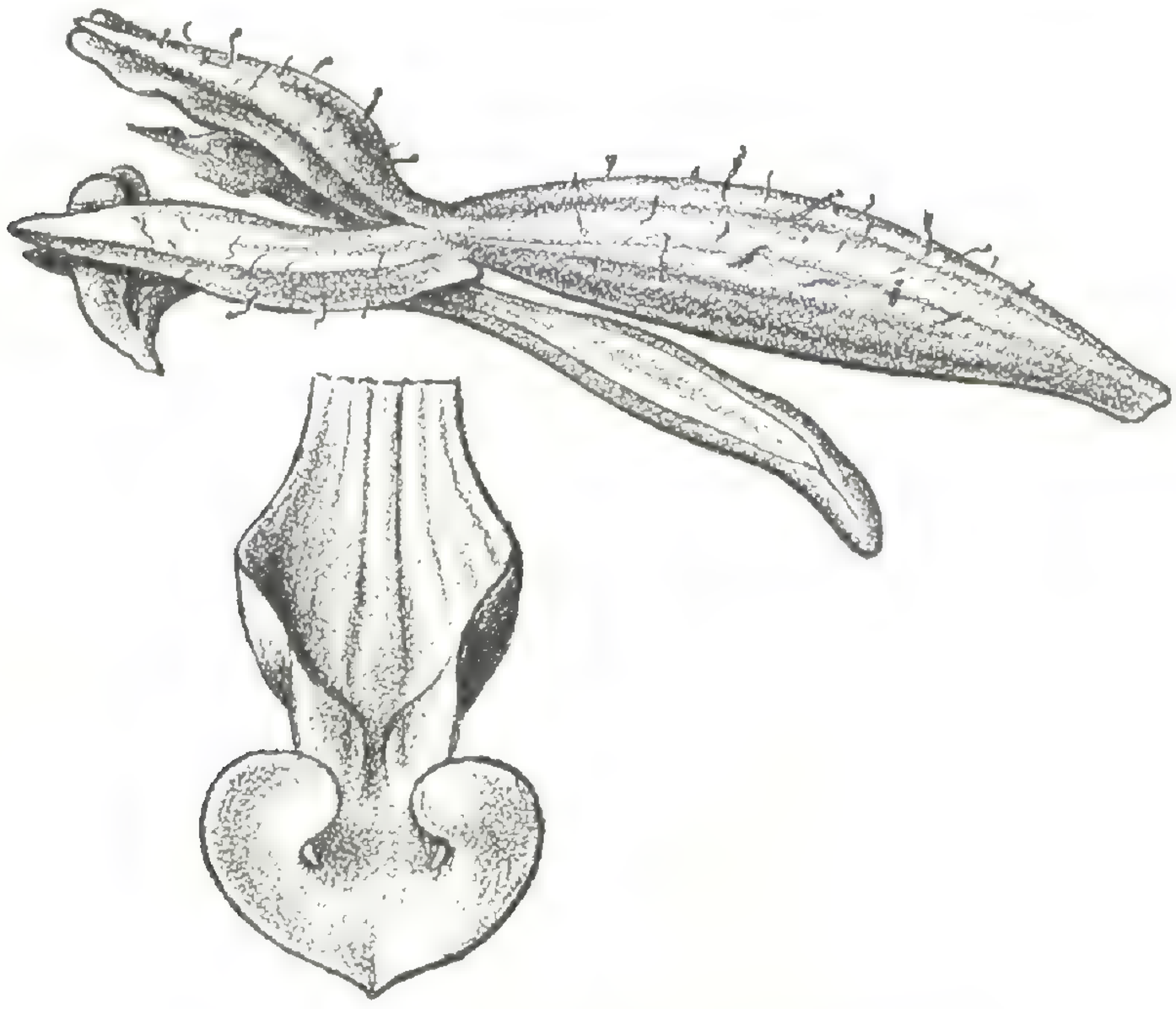
This new species may be compared with the Colombian *Erythrodes zeuxinoides* (Schltr.) Ames, but differs from it in having much smaller flowers and a very dissimilar lip. The flowers, judged from the specimen, are greenish-white in color.

Colombia: Departamento del Magdalena, Cordillera Oriental, Sierra de Perijá, 6 km. east-northeast of Manaure, 42 km. east of Valledupar, 7 km. from the Venezuelan border. 2100 meters alt. Feb. 1, 1945. *Martin L. Grant 10748* (Type in U.S. Nat. Herb. no. 2107290).

Ecuador: Chimborazo, Riv. Chasuan. *R. Spruce 6138*. Herb. Reichenbach nos. 37766, 37767.

Erythrodes xystophylloides *Garay sp. nov.*

Terrestris, erecta, 20–25 cm. alta; rhizomate cauliformi, repenti; radicibus ex internodiis orientibus, filiformibus, leviter flexuosis, sparse pubescentibus; caulibus erectis, primum remote vaginatis, deinde 4–6-foliatis; foliis anguste lanceolatis, subacutis vel acuminatis, basi attenuatis, deinde in vaginas dilatatis transeuntibus;



Erythrodes xystophylloides *Garay*

lamina 2.5–3 cm. longa, 4–5 mm. lata; pedunculo erecto, remote 3-vaginato; racemo pauci- (6-8-) floro; bracteis lanceolato-setaceis, ovariorum pedicellatorum dimidium aequantibus; floribus in genere inter minores, albidis; sepalo postico ovato, obtuso, valde concavo, uninervio, extus sparse pilosulo, 5 mm. longo, 1.75 mm. lato; sepalis lateralibus ovato-oblongis, leviter obliquis, obtusis, extus sparse pilosis, uninerviis, 5 mm. longis, 1.5 mm. latis; petalis oblique spathulatis, uninerviis, glabris, quarta parte apicali sese tegentibus et conglutinatis, 5 mm. longis, 1 mm. latis; labello conduplicato, e basi elliptico-cucullato apice in laminam anchoriformem rotundatam subito dilatato, 5 mm. longo, in medio 2 mm., apice 4 mm. lato; calcare gracili, 4 mm. longo, 1 mm. crasso.

In general appearance this new species seems to be a miniature form of *Erythrodes aystophylla* (Rchb.f.) Ames. These two species may be distinguished from each other, apart from size, by the shape of the lip, which is bilobed in *E. aystophylla* and anchoriform in the new concept. In natural position, the lip is conduplicate-cucullate with the anchoriform tip reflexed and rolled inwardly.

COLOMBIA: Dept. Cundinamarca; Cordillera Oriental, Ojo de Agua, south side Guavio River, 32 km. east of Gachalá. 2035 meters alt. Nov. 1, 1944. *Martin L. Grant 10557* (TYPE in Herb. Ames no. 69102; DUPLICATE TYPE in U.S. Nat. Herb.).

Stelis nexipous *Garay sp. nov.*

Epiphytica, caespitosa, usque ad 25 cm. alta; radicibus filiformibus flexuosis, glabris; caulibus secundariis erectis vel paulo arcuatis, vaginis 3 alte amplectentibus maxima pro parte obtectis, 6-12 cm. longis; folio coriaceo, oblongo-ligulato, apice obtusiusculo, basi in petiolum brevem sensim angustato, petiolo incluso 6–10 cm. longo, 0.7–1.2 cm. lato; inflorescentia singula, erecta vel interdum paulo arcuata, usque supra basim multiflora, 8–14

cm. longa; bracteis infundibuliformibus, acutiusculis, quam ovaria pedicellata longioribus, 3–4 mm. longis; sepalis lateralibus inter se liberrimis sed cum sepalo postico maxima pro parte in synsepalum connatis; synsepalo antice 3-lobo, per lobum 3-nervio, intus minutissime hirsutulo, ad basim leviter cochleato, 1–1.3 cm. longo, inter lobis laterales 1 cm. lato; petalis valde carnosis, cuneato-flabellatis, obtusis, dimidio superiore valde incrassatis, basi 3-nerviis, 0.75 mm. longis, 1.25 mm. latis; labello valde carnoso, triangulari, basi valde incrassato, ante incrassationem leviter excavato, 0.75 mm. longo latoque; columna humili, crassa, sursum abrupte dilatata, brachiis divaricatis; ovario cum pedicello, 2–3 mm. longo.

Stelis nexipous is rather peculiar in the shape of its sepals. In appearance it does not resemble any other species in the genus. The genus *Physothallis*, which was established on a similar monosepalous character, has a column typical of the genus *Physosiphon*, and I am now convinced that the two genera are inseparable. However, the concept *Physothallis* is just as abnormal in the genus *Physosiphon* as the species described herein is in the genus *Stelis*. A few more cases like that of *S. nexipous* will help to confirm my feelings that we are dealing in the *Pleurothallidinae* with a very natural biological unit or genus which encompasses all the generic concepts proposed up-to-date within that subtribe.

Ecuador: Prov. Napo-Pastaza, Mera, towards Mangayacu; epiphyte in rastrojo. Ca. 1100 m. alt. March 7, 1956. *Erik Asplund 19638* (Type in Herb. State Mus. Nat. Hist., Stockholm, Sweden; Duplicate type in Herb. Ames).

Platystele ornata *Garay sp. nov.*

Epiphytica, caespitosa, pusilla, usque ad 2.5 cm. alta; radicibus filiformibus flexuosis, glabris; caulibus secundariis vix rite evolutis, ullis, vagina unica omnino obtectis; folio obovato-spathulato, apice obtuso, ca. 2 cm.

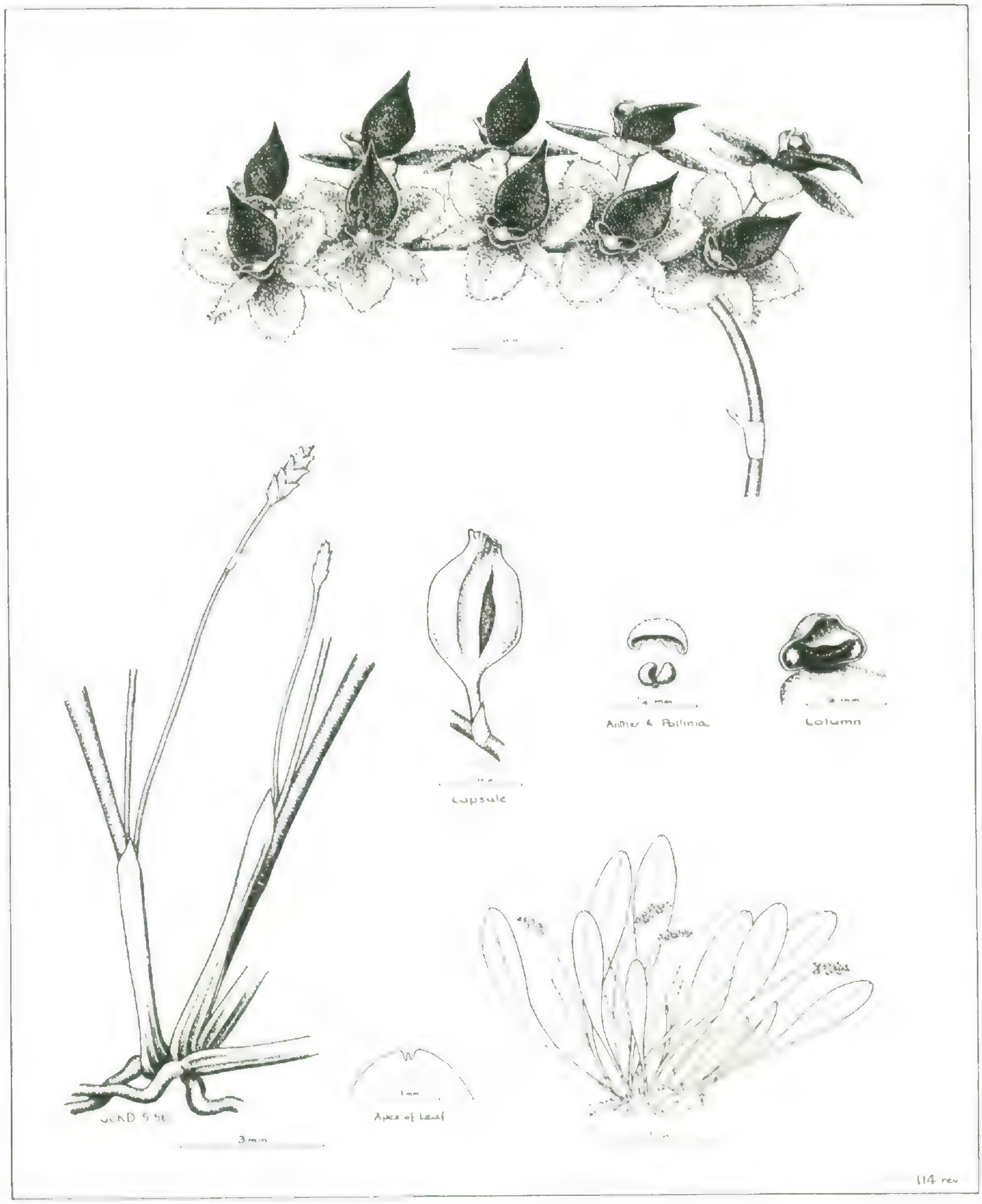
EXPLANATION OF THE ILLUSTRATION

PLATE XXXV. STELIS NEXIPOUS *Garay*. 1, plant, one half natural size. 2, flower, three times natural size. 3, petal, fifteen times natural size. 4, lip, twenty times natural size.

Drawn by ELMER W. SMITH

STELIS
nexipous
Garay
1
2
3
4

Plate XXXVI



Platystele ornata *Garay*

Drawn by G. C. K. Dunsterville

longo, 3 mm. lato; inflorescentia capillari, erecta vel paulo arcuata, subdense pluriflora, ca. 2 cm. longa; bracteis infundibuliformibus, 0.1 mm. longis; sepalis ovatis, acutis, extus sparse glanduloso-pilosulis, ca. 0.5 mm. longis; petalis obovatis, apice acutis, margine glanduloso-pilosulis, sepalis paulo brevioribus; labello ovato-lanceolato, leviter cochleato, apice acuminato, sepalis magnitudine, disco nudo; columna humili, crassa, generis; ovario cum pedicello quam bracteis longiore.

This new species is easily separable from the others in the genus by its glandular-hirsute floral segments.

VENEZUELA: New road, Santa Teresa to Altagracia. Dec. 28, 1953. *G. C. K. Dunsterville 114* (TYPE in Herb. Ames).

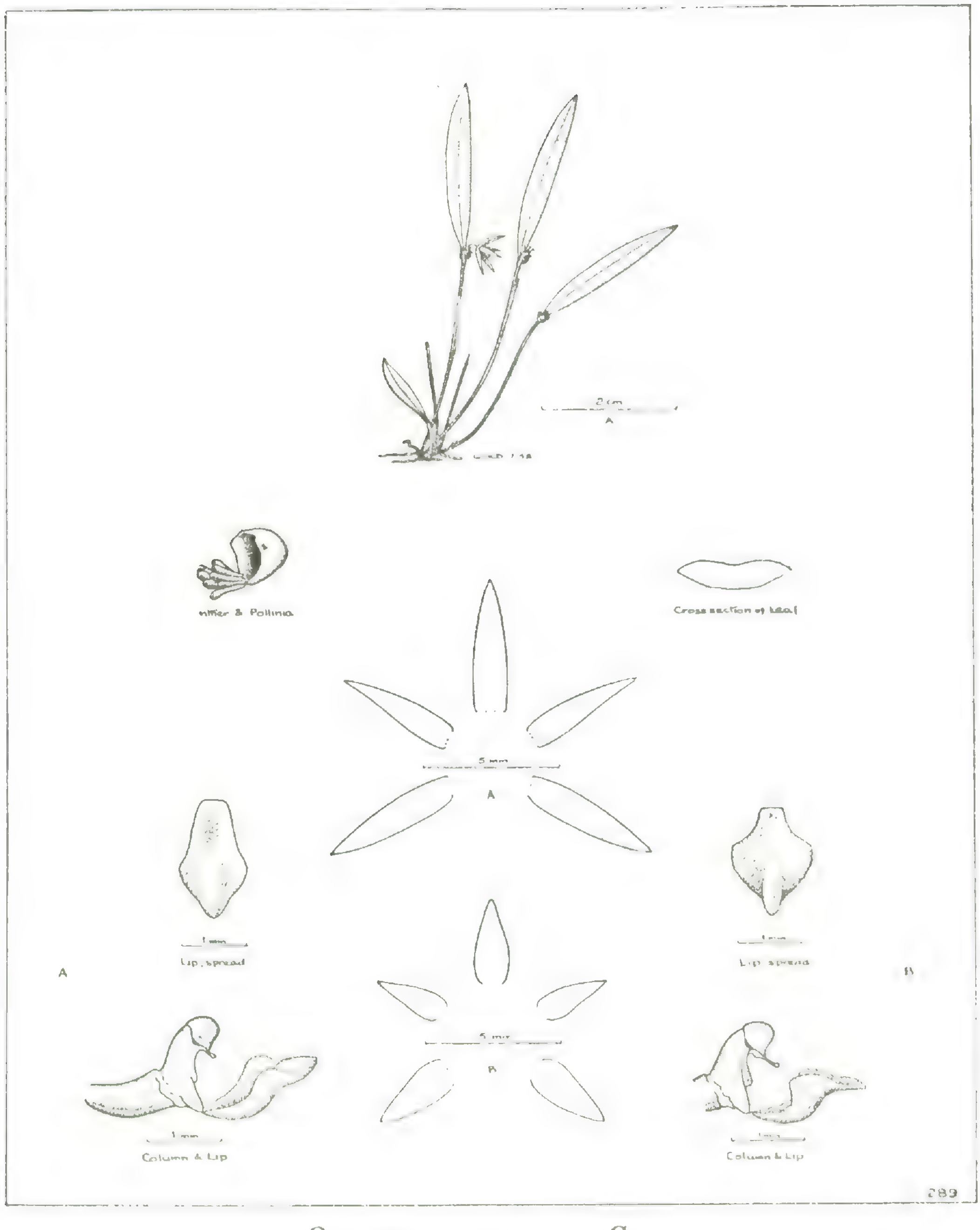
Octomeria deltoglossa *Garay sp. nov.*

Epiphytica, caespitosa, usque ad 8 cm. alta; radicibus filiformibus, flexuosis, glabris; caulibus secundariis erectis vel paulo arcuatis, vaginis 3, arcte adpressis omnino obtectis, 2–5 cm. longis; folio carnoso, oblongo-ligulato vel oblongo-lanceolato, apice acuto vel acutiusculo, basim versus sensim angustato, 2–4 cm. longo, 1–3 mm. lato; floribus aggregatis, diaphanis; sepalis inter se simillimis, ovatis vel oblongo-ovatis, acutis, 3–5 mm. longis, 1–1.5 mm. latis; sepalis lateralibus paulo obliquis; petalis sepalis simillimis sed paulo minoribus, 3–4.5 mm. longis, 1–1.2 mm. latis; labello valde carnoso, deltoideo, apice acuto et pulvinato-incrassato, 1.5–1.8 mm. longo, 1–1.3 mm. lato; columna crassa, arcuata; ovario pedicellato ca. 2 mm. longo.

This new species is closely related to the Brazilian *Octomeria rhodoglossa* Schltr., but differs from it in having smaller flowers and a dissimilar lip.

VENEZUELA: Río Carrao. *G. C. K. Dunsterville 289* (TYPE in Herb. Ames).—Territorio Amazonas, Cerro Sipapo (Paraque), 1400 m. alt. *B. Maguire & L. Politi 27727* (Herb. N.Y. Bot. Gard.).

Plate XXXVII



Octomeria deltoglossa *Garay*

Drawn by G. C. K. Dunsterville

Malaxis tipuloides (*Lindl.*) *O. Ktze.* var. **exigua** *Garay var. nov.*

A typo floribus multo minoribus differt. Planta usque ad 30 cm. alta; foliis 5, basilaribus, aggregatis, ovato-lanceolatis, acutis vel subacuminatis, 12–13 cm. longis, 1–1.5 cm. latis; racemo erecto, densissime multifloro; bracteis lanceolato-setaceis, pedicellis aequilongis; floribus parvulis; forma sepalorum et petalorum et labelli illa typi simillima; sepalis tantum 4–5 mm. longis.

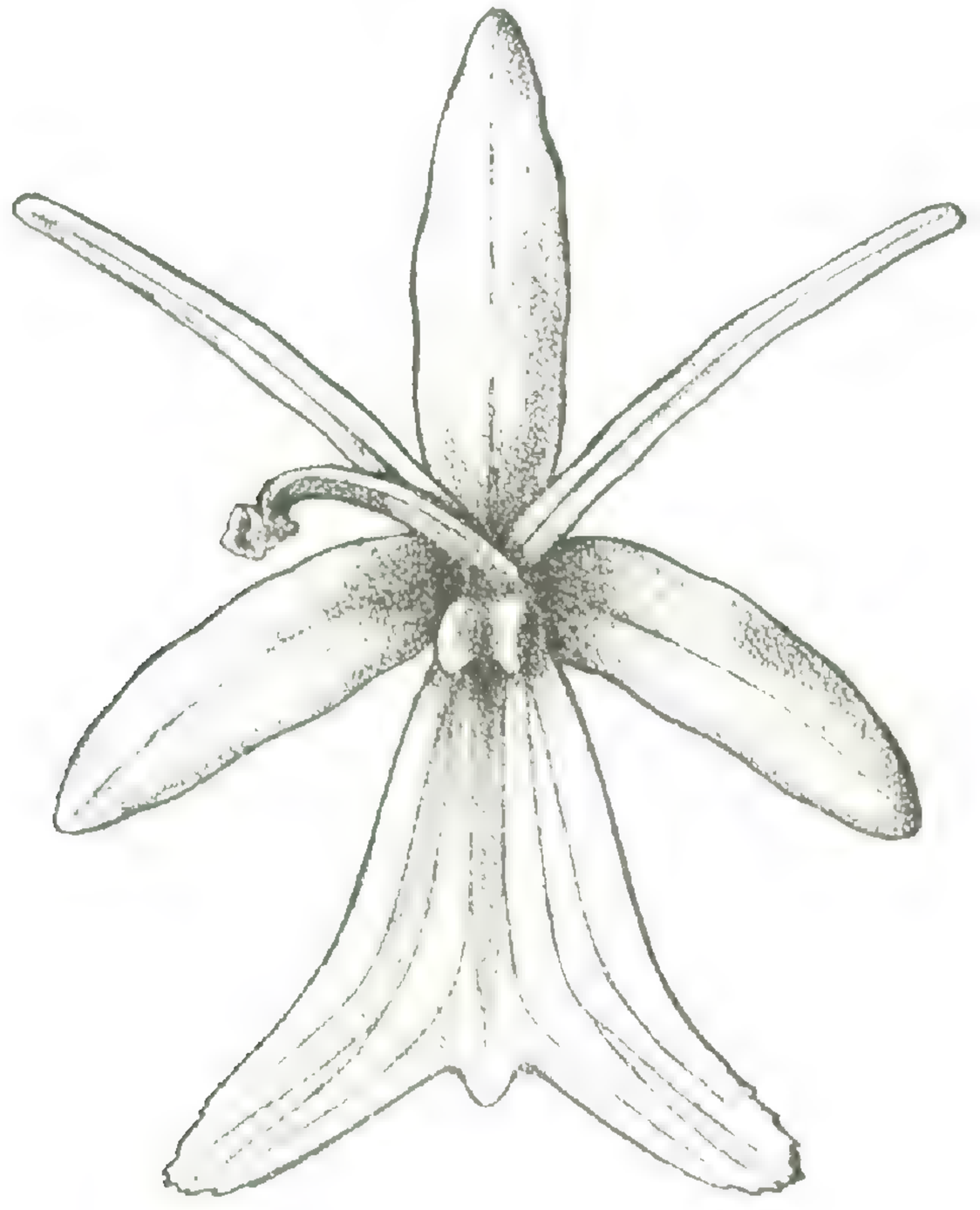
Whether to recognize this collection as a new species or merely as a variety of *M. tipuloides* was a matter of deliberation for a long time. No morphological differences of specific value can be observed in the floral structures between this collection and the typical species. However, the small dimensions are so striking that I feel it necessary to establish it at least as a variety.

COLOMBIA: Dept. Cundinamarca. Cordillera Oriental; Hato Grande, east side of Río Muchindote, 13 km. east of Gachetá. 2600 meters alt. June 14, 1944. *Martin L. Grant 9456.* Collected under the auspices of the U.S. Foreign Economic Administration: Colombian Cinchona Mission (TYPE in Herb. Ames; DUPLICATE TYPE in U.S. Nat. Herb.).

Liparis serpens *Garay sp. nov.*

Terrestris, 5–8 cm. alta; rhizomate satis gracili, flexuoso, prorepenti, vaginis remotis, scariosis, cucullatis, acutis, 7–10 mm. longis obsesso; folio juxta basim pseudobulbi singulo, prominenter petiolato, lamina ovato-cordata, acuta vel subacuminata, basi abrupte rotundata, margine leviter crispata, petiolo incluso 3–5.5 cm. longa, 1.5–3 cm. lata; pseudobulbo vix evoluto, ca. 5–7 mm. longo; inflorescentia singula, erecta vel leviter arcuata, satis gracili, 4.5–8 cm. longa, dimidio superiore dense multiflora; bracteis ovato-lanceolatis, acutis, quam ovariis pedicellatis brevioribus, 3–4 mm. longis; sepalis ovatis, obtusis, margine revolutis, nervo mediano prominenti,

4.5–5 mm. longis, 1.25 mm. latis; sepalis lateralibus leviter obliquis; petalis ligulatis, margine revolutis, uninerviis, 5 mm. longis, 0.3 mm. latis; labello a basi cuneata subito dilatato, antice bilobo, in medio apiculato; lobis divergentibus oblongis, margine exteriore apicem versus serrulato-denticulata; disco in medio leviter in-



LIPARIS SERPENS *Garay*

crassato, ad basim callo transverse semiquadrato, antice leviter excavato ornato, 6 mm. longo, in medio 3 mm. lato, inter lobos apicales 6 mm. lato; columna gracili, leviter arcuata, apice incrassata auriculataque, ca. 3 mm. longa; ovario cum pedicello alato, ca. 5 mm. longo.

Liparis serpens is closely related to *L. neuroglossa* Rchb.f. and *L. elegantula* Kränzl. It differs from the former in its trailing habit and in the shape of the lip. *Liparis elegantula*, which is very similar vegetatively, appears to be constantly bifoliate and to have a differently shaped lip.

COLOMBIA: Dept. Cundinamarca, Quebrada del Chicó, Bogotá. Terrestrial in shady woods. Flowers light green, lip bright green with violet veins. 2700–2800 meters alt. *Martin Schneider 95* (TYPE in Herb. Ames no. 68507.)

Epidendrum superpositum *Garay sp. nov.*

Epiphytica, ramosa, usque ad 40 cm. alta; radicibus crassiusculis, glabris; caulibus superpositis, erectis vel paulo arcuatis, vaginis amplis omnino obtectis, apice 2–3-phyllis; foliis ovatis, acutis, satis coriaceis, 3–6 cm. longis, 0.8–1.4 cm. latis; pedunculo abbreviato, 1–2 cm. longo; racemo densifloro, subcapitato, recurvo; bracteis setaceis ovariis brevioribus; sepalo postico obovato, apice acuto, 3-nervio, 8–10 mm. longo, 3–4 mm. lato; sepalis lateralibus obliquis, obovato-falcatis, apice cuspidatis, 3-nerviis, 8–10 mm. longis, 4–6 mm. latis; petalis linearibus obovatis, obtusis, 1-nerviis, 8–10 mm. longis, 1–1.5 mm. latis; labello trilobo, lobis lateralibus late rotundatis, margine leviter undulatis, lobo terminali antico, in medio exciso, sic bilobulato, disco basi bicalloso, 5–8 mm. longo, 10–12 mm. lato; columna labello adnato; ovario cum pedicello ca. 1.5 cm. longo.

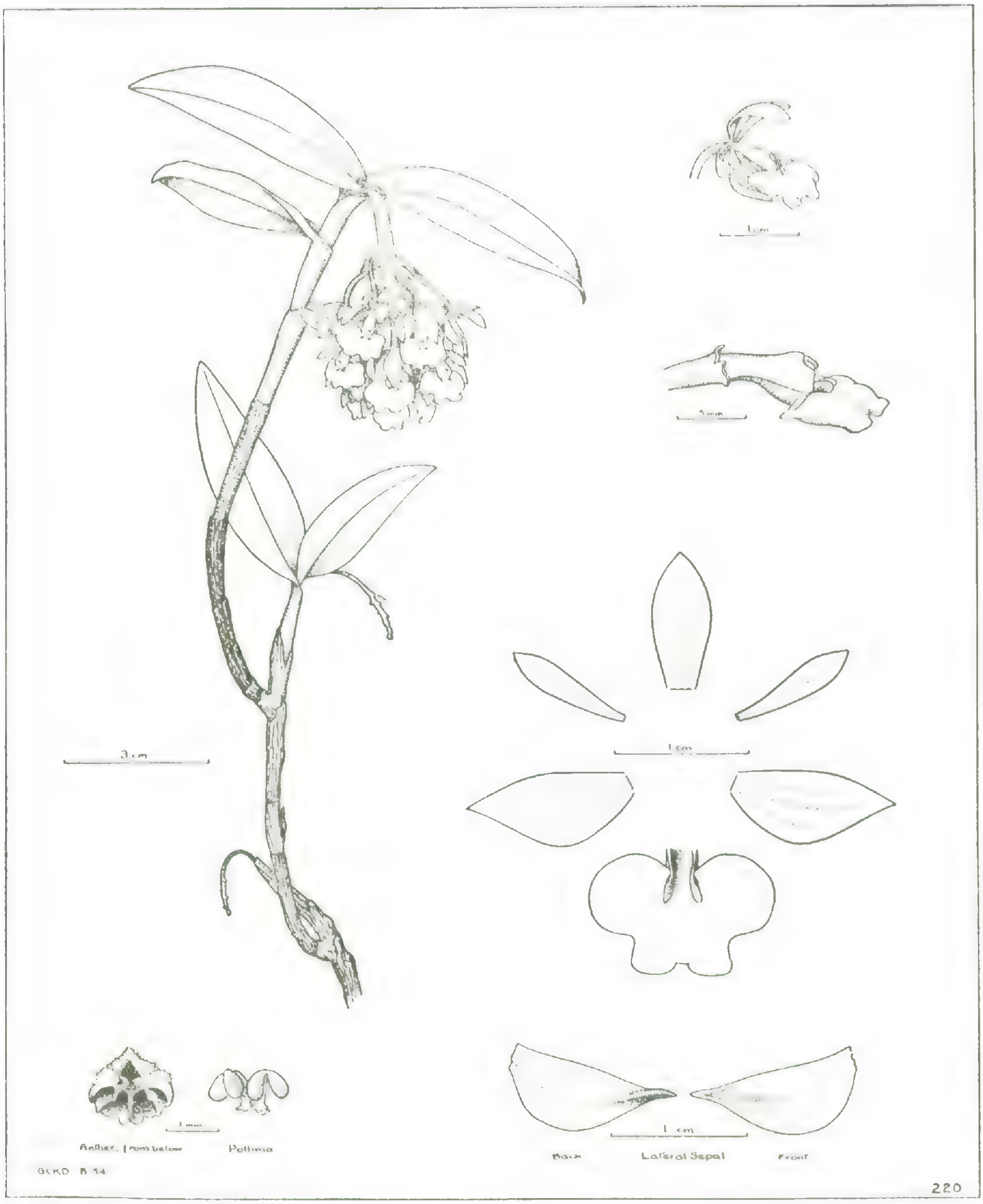
This new species is apparently similar in appearance to *Epidendrum obliquum* Schltr., *E. soratae* Rchb.f. and *E. Steinbachii* Ames, but it differs from them in various floral structures, especially in the shape of the lip.

VENEZUELA: Junquito. *G. C. K. Dunsterville 220* (TYPE in Herb. Ames no. 68942).

Hexadesmia Dunstervillei *Garay sp. nov.*

Epiphytica, caespitosa vel prolifera, usque ad 20 cm. alta; radicibus filiformibus, flexuosis, glabris; pseudobulbis longe stipitatis, cylindraceis, bifoliatis, usque ad 6 cm. longis; foliis ellipticis vel oblongo-ellipticis, utrinque attenuatis, apice acutis, 2–7 cm. longis, 0.7–2 cm. latis; inflorescentia satis abbreviata, pauci- (1–2-) flora:

Plate XXXVIII



Epidendrum superpositum *Garay*

Drawn by G. C. K. Dunsterville

Plate XXXIX

Hexadesmia Dunstervillei *Garay*

Drawn by G. C. K. Dunsterville

bracteis ovato-lanceolatis, acuminatis, ca. 2.5 mm. longis; sepalis lanceolato-ovatis, acuminatis, 5-7-nerviis; sepalo postico 15–16 mm. longo, 4–6 mm. lato; sepalis lateralibus leviter obliquis, 15–16 mm. longis, 4–5 mm. latis; petalis ovato-lanceolatis, acuminatis, 15–16 mm. longis, 6–7 mm. latis; labello subquadrato-flabellato, apice acuto, disco bicarinato, 14–15 mm. longo, 8-9 mm. lato; columna leviter arcuata, basim versus paululo dilatata et in pedem brevissimum producta.

Hexadesmia Dunstervillei closely resembles *H. Jimenesii* Schltr. from Costa Rica but is easily separable from that taxon by the shape of the lip. This new species is dedicated to my good friend G. C. K. Dunsterville, President of the Shell Oil Co. in Venezuela, with whom I am preparing an iconography of the Orchids of Venezuela.

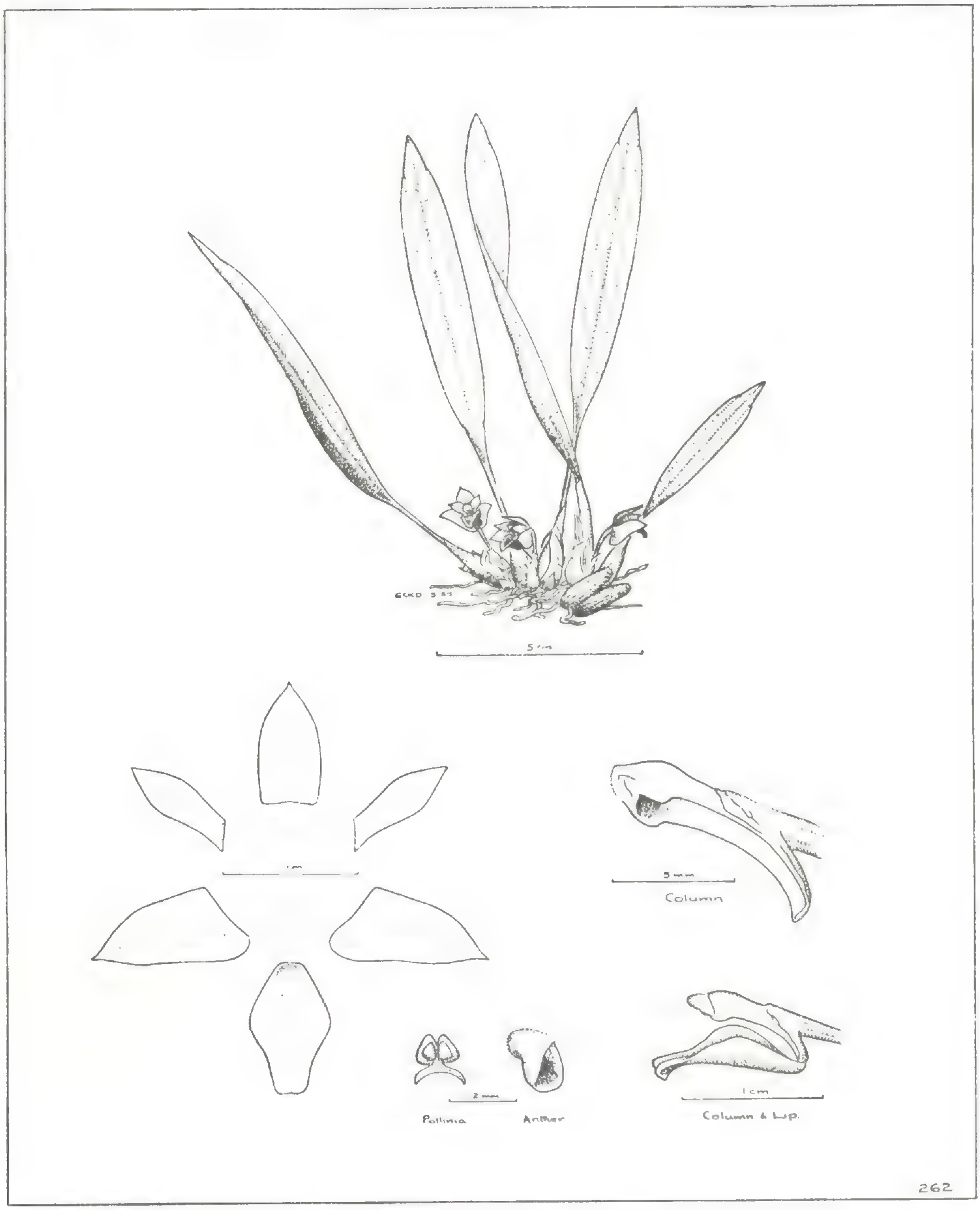
Venezuela: Estado Miranda, Santa Teresa, Guatopo. Dec. 31, 1955. *G. C. K. Dunsterville 336* (Type in Herb. Ames).

Bifrenaria minuta *Garay sp. nov.*

Epiphytica, caespitosa, minuta, usque ad 12 cm. alta; radicibus filiformibus leviter flexuosis, glabris; pseudobulbis aggregatis, ovoideis, unifoliatis, 1.5–2 cm. altis; folio pergameneo, subplicato, apice acuto, basi in petiolum 2–3 cm. longum attenuato, petiolo incluso 10–12 cm. longo, 1–1.5 cm. lato; inflorescentia juxta basim pseudobulborum nata, uniflora; pedunculo capillari, ca. 1–1.5 cm. longo; sepalo postico ovato-oblongo, apice acuto, 5-nervio, 9 mm. longo, 4.5 mm. lato; sepalis lateralibus oblique ovatis vel ovato-oblongis, apice acutis, 5-nerviis, 10 mm. longis, 6 mm. latis; petalis trulliformibus apice acutis, 3-nerviis, 8.5 mm. longis, 3 mm. latis; labello rhombeo, antice truncato, disco vix calloso, 10 mm. longo, 6 mm. lato; columna leviter clavata, basi in pedem producta; ovario cum pedicello ca. 6 mm. longo.

This new species is quite unique in the genus on ac-

Plate XL



Bifrenaria minuta *Garay*

Drawn by G. C. K. Dunsterville

count of the extremely small flowers. It is apparently a borderline species between *Bifrenaria* and *Maxillaria*.

VENEZUELA: Río Carrao. *G. C. K. Dunsterville 262* (TYPE in Herb. Ames.)

Bifrenaria grandis (*Kränzl.*) *Garay comb. nov.*

Lacaena grandis Kränzl. in Fedde Repert. 25 (1927) 25.

An examination of an isotype (*Buchtien 501*) in the U.S. National Herbarium reveals that Kränzlin's concept is a member of the genus *Bifrenaria*, section *Lindleyella*, and is closely allied to the Colombian *B. picta* (Schltr.) Schweinf. *Bifrenaria grandis* is native of Bolivia.

Maxillaria equitans (*Schltr.*) *Garay comb. nov.*

Camaridium equitans Schltr. in Fedde Repert. Beih. 7 (1920) 176.

Marsupiaria equitans Hoehne in Arquiv. Bot. Est. S. Paulo 2, pt. 4 (1947) 71.

A recent collection (*Cuatrecasas 22092*) from the Departamento del Valle in Colombia shows that this species has somewhat falcate leaves, similar to those of *M. vandiformis* Schweinf., a character not mentioned by Schlechter in the original description. Since *Camaridium* is not tenable, the above transfer is proposed.

Maxillaria Sophronitis (*Rchb.f.*) *Garay comb. nov.*

Ornithidium Sophronitis Rchb.f. in Bonpl. 2 (1854) 18.

This rather showy species has not previously been transferred to the genus *Maxillaria*. It is known from Venezuela only and has recently been collected by Mr. Dunsterville (*Dunsterville 388*).

Scelochilus corydaloides (*Kränzl.*) *Garay comb. nov.*

Rodriguezia corydaloides Kränzl. in Fedde Repert. 25 (1928) 24.

An examination of the type (*Buchtien 528*) indicates that this taxon is referable to the genus *Scelochilus*.

Rodriguezia Teuscheri *Garay sp. nov.*

Epiphytica, caespitosa, ca. 12 cm. alta; radicibus flexuosis, glabris; pseudobulbis ovoideis, lateraliter compressis, unifoliatis, 2–3 cm. longis; folio coriaceo, elliptico vel oblongo-elliptico, canaliculato, apice acutiusculo, basi in petiolum brevem producto, 8–10 cm. longo, 2.5–3 cm. lato; inflorescentia juxta basim pseudobulborum nata, erecta vel paulo arcuata, pauciflora, ca. 8 cm. longa; bracteis ovatis, acutis, ca. 5 mm. longis; sepalo postico valde concavo, obovato, apice obtusiusculo, 1.5 cm. longo, ca. 1 cm. lato; sepalis lateralibus usque ad apicem connatis, reflexis, concavis, falcatis, ca. 2.5 cm. longis; petalis obovato-spathulatis, apice obtusis vel subtruncatis, 1.5 cm. longis, 1 cm. latis; labello in ambitu trapezoideo, antice emarginato, in medio sinuato, basi in processum carnosum producto, disco per totam longitudinem lamellis 2, parallelis ornato; lamina labelli ca. 2 cm. longa, antice 1.5 cm. lata; columna clavata, satis gracili, ca. 1.7 cm. longa; ovario cum pedicello ca. 2.5 cm. longo.

The specific name is given in honor of Dr. Henry Teuscher, Curator of the Montreal Botanical Garden, Canada, whose keen interest in and knowledge of orchidology is widely known and recognized.

Ecuador: 100 km. from Guayaquil. *H. Teuscher s.n.* (Type in Herb. Ames). Flowered in cultivation at the Montreal Botanical Garden.

Cryptocentrum Lehmannii (*Rchb.f.*) *Garay comb. nov.*

Aëranthus (*Cryptoplectri*) *Lehmanni* Rchb.f. in Otia Bot. Hamb. (1878) 10.

EXPLANATION OF THE ILLUSTRATION

PLATE XLI. Habit photograph of RODRIGUEZIA TEUSCHERI *L. A. Garay*. This is a photograph of the type material as cultivated in the Montreal Botanical Garden, Canada.

Photograph by ROMEO MELOCHE

Plate XLI

Campylocentrum Lehmanni (Rchb.f.) Schltr. in Fedde Repert. Beih. 8 (1921) 164.

An excellent record of the type of the Ecuadorian *Aëranthus Lehmanni* in the Ames Herbarium reveals that this concept is undoubtedly referable to the genus *Cryptocentrum*. Apparently *C. Jamesonii* Benth. is the only other species of the genus which has been reported from Ecuador. Although these two taxa seem to be very similar vegetatively, *C. Lehmannii* may be separated by the presence of six to seven sheaths on the peduncle in contrast to one or two in *C. Jamesonii*, as well as by the pandurate and long-acuminate lip in the former, whereas it is ovate in the latter.

In his system of the *Orchidaceae*, Schlechter assigned the genus *Cryptocentrum* to the subtribe *Maxillaricae*. In view of the peculiar vegetative and floral structures, however, I cannot agree with this opinion. We find here a type of vegetative growth closely resembling a monopodial development. The leaves are arranged distichously on a shortened stem, but only a few terminal ones seem to be persistent, at least during anthesis, while the lower part of the stem bears the remnants of the sheathing bases of the leaves of previous years. The one-flowered peduncles are always borne in the axils of these sheathing bases on the lower portion of the stem. This condition is observable in every species assigned to *Cryptocentrum*, with the exception of *C. pseudobulbosum* Schweinf. In *C. pseudobulbosum*, we find, in addition, a well developed pseudobulb, quite an unusual condition, but, from the systematic point of view, exceedingly important. With the evidence from *C. pseudobulbosum*, it is obvious that this genus has to be kept among the genera with sympodial growth. It may be mentioned as a mere curiosity that this vegetative growth is entirely homologous with that of the old world genus *Phreatia*.

In the floral structure of *Cryptocentrum*, furthermore, we find evidence of a more complex nature than would be normal for the subtribe *Maxillarieae*. The lateral sepals are connivent at the base and form a very prominent sepaline spur to which the claw of the lip is internally adnate for its entire length. This feature is observable in the genus *Sepalosiphon* in addition to *Cryptocentrum*. (*Sepalosiphon* is known only from New Guinea.) Though we have here a striking homology in floral structures, the two genera are vegetatively very dissimilar. In both cases the column is very short, more or less petaloid and without a foot. The incumbent anther rests on a more or less ascending and acicular rostellum.

In applying these observations to Schlechter's "*Systema Orchidacearum*," we find that the characters of the subtribe *Maxillarieae* are very different, as shown in the following tabular comparison.

Maxillarieae	Cryptocentrum
Rostellum not evident.	Rostellum prominent.
Column elongate and with a definite foot which forms, with the lateral sepals, a more or less prominent mentum.	Column short and footless. No mentum present.
Lateral sepals not spurred.	Lateral sepals spurred.
Lip articulate with the column foot; disc with a longitudinal callus.	Lip adnate to the spur; disc ecallose.

It is clear that *Cryptocentrum* cannot be maintained in the subtribe *Maxillarieae*. In following through Schlechter's system, the characters of *Cryptocentrum* as tabulated above, give us substantial ground to warrant the erection of a new subtribe, which should be placed between *Ornithocephaleae* and *Saundersieae*.

Cryptocentreae *Garay subtribus nova.*

Pollinia 4. Plantae epiphyticae, pusillae. Pseudobulbi rudimentarii vel deficientes. Caules satis abbreviati, pseu-

domonopodium formantes. Folia disticha. Inflorescentiae uniflorae. Sepala calcarata. Labellum sepalorum calcari intus adnatum. Columna apoda. Rostellum prominens, aciculare. Stipes polliniorum abbreviata.

Genera: *Cryptocentrum* Bentham.
Anthosiphon Schlechter.

Notylia Norae *Garay sp. nov.*

Epiphytica, pusilla, ca. 2.5 cm. alta; radicibus filiformibus, flexuosis, glabris; foliis equitantibus, oblique ovato-lanceolatis, carnosis, 5–8 mm. longis, 1.5 2 mm. latis; inflorescentia erecta vel paulo arcuata, pauciflora; bracteis ovatis, acutis, ca. 1 mm. longis; floribus diaphanis, lilacinis; sepalo postico ovato, conduplicato, apice acuto, 1-nervio, 3 mm. longo, 1.7 mm. lato; sepalis lateralibus liberis, anguste oblongo-lanceolatis, acutis, 1-nerviis, 4 mm. longis, 0.8 mm. latis; petalis ovato-lanceolatis, acutis, 1-nerviis, 4 mm. longis, 1 mm. latis; labello longe unguiculato, deinde in laminam ovatam in medio leviter constrictam expanso, apice acuto, basi minutissime ciliato, 3-nervio, 3.5 mm. longo, antice 1.8 mm. lato; columna erecta, capitata, ca. 2 mm. longa; ovario cum pedicello ca. 2.5 mm. longo.

Notylia Norae is related to the Bolivian *N. lilacina* Kränzl. but differs from it in the shape of the petals and lip.

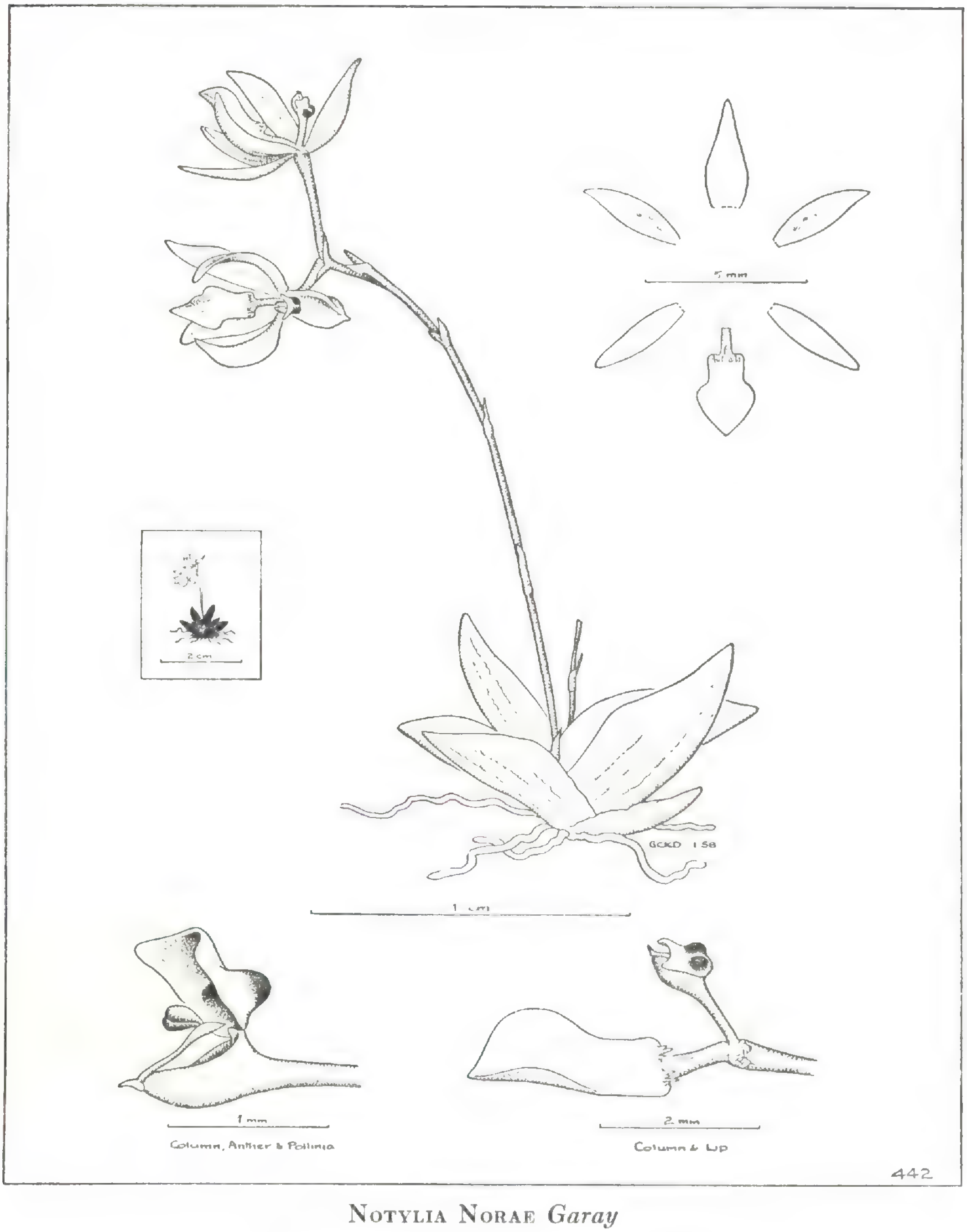
It gives me great pleasure to dedicate this beautiful miniature orchid to Mrs. Dunsterville, whose inspiration and special interest in botanicals has been of indispensable help in the preparation of the Iconography of the Venezuelan Orchids.

Venezuela: Kavanupa, Río Uaiparu. On small tree near water's edge. *G. C. K. Dunsterville 442* (Type in Herb. Ames).

Telipogon Teuscheri *Garay sp. nov.*

(§ *Brevicaules*). Radicibus satis longis, copiosis; cauli-

Plate XLII



Notylia Norae *Garay*

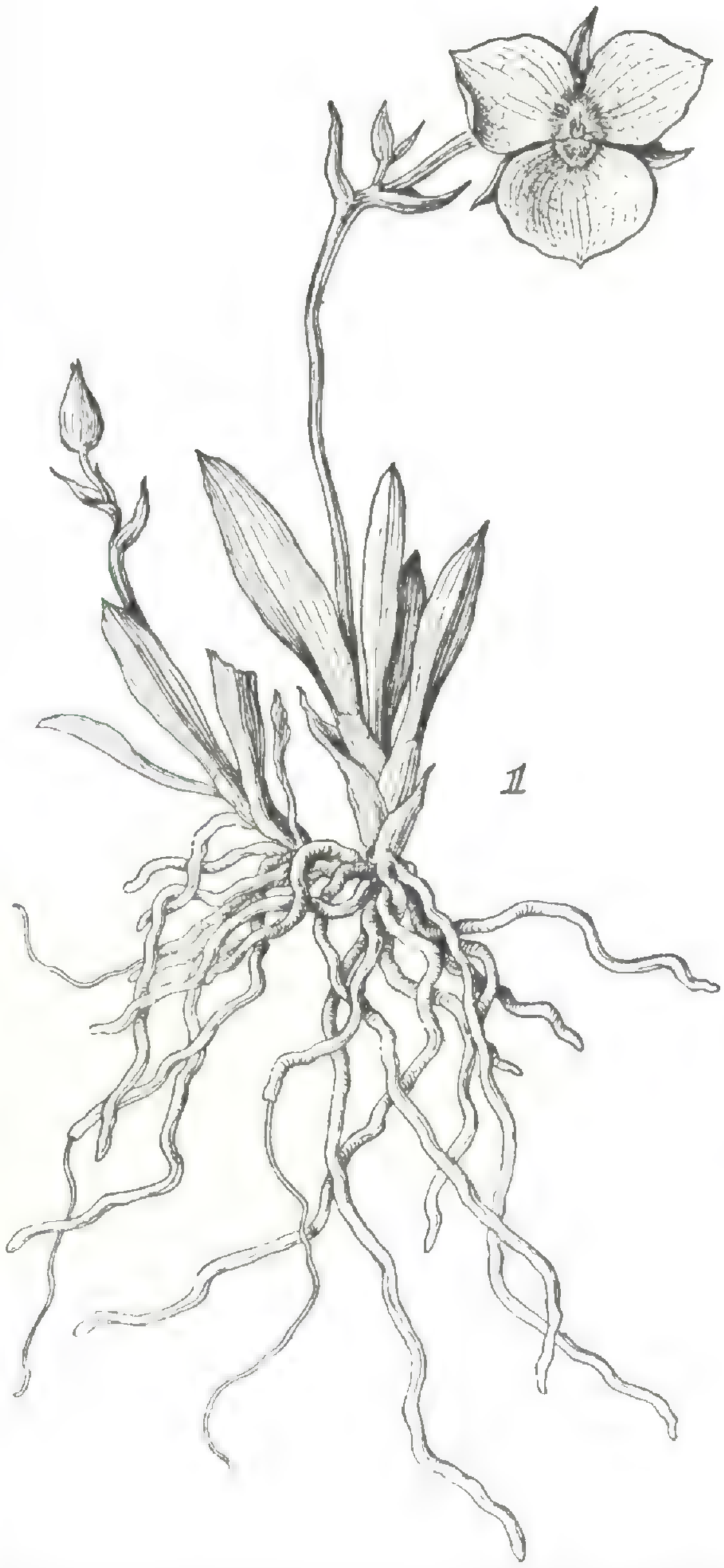
Drawn by G. C. K. Dunsterville

EXPLANATION OF THE ILLUSTRATION

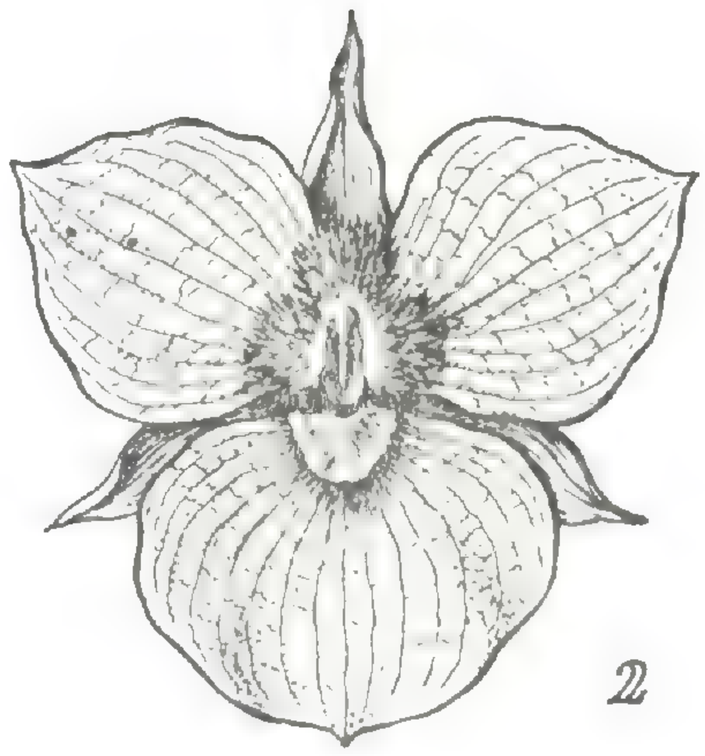
PLATE XLIII. TELIPOGON TEUSCHERI *Garay*. 1, plant, two thirds natural size. 2, flower, expanded, slightly enlarged. 3, lip, twice natural size.

Drawn by ELMER W. SMITH

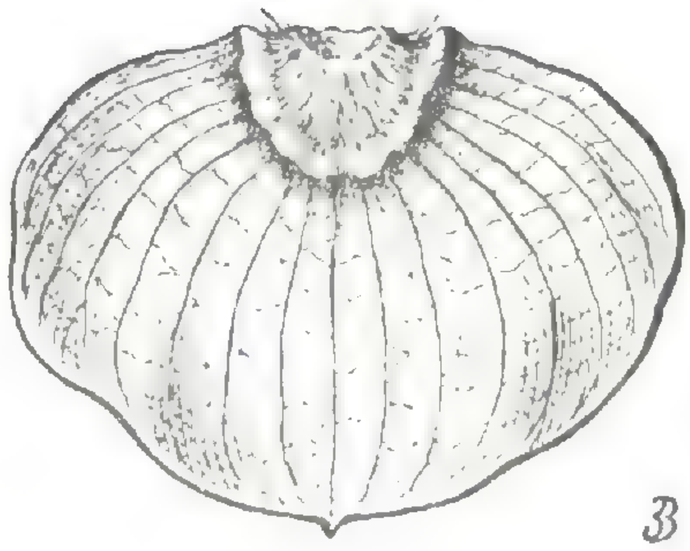
TELIPOGON Teuscheri Garay



1



2



3

E.W.Smith

bus abbreviatis, ca. 4-foliatis; foliis satis carnosis, oblongo-lanceolatis, acutis, basi articulatis, 2.5–4 cm. longis, 4–8 mm. latis; inflorescentiis erectis, vel leviter flexuosis, quam foliis duplo longioribus, apice 2–4-floris; pedunculo compresso, alato, usque ad 7 cm. longo; bracteis ovato-lanceolatis, dorso leviter carinatis, ovariis duplo brevioribus; floribus in genere inter mediocres; sepalis ovato-triangularibus, acutis, 3-nerviis, dorso prominenter carinatis, 14 mm. longis, supra basim 6 mm. latis; petalis rhombeo-ovatis, acutis vel subacuminatis, 11-nerviis, 16 mm. longis, 13 mm. latis; labello transverse subrotundo, acuto, in medio breviter apiculato, 17-nervio, 13 mm. longo, 17 mm. lato; disco basim callo deltoideo, hirsuto ornato; columna humili, hispido-setacea; ovario graciliter pedicellato, cum pedicello ca. 2 cm. longo.

Telipogon Teuscheri differs from *T. semipictus* Rchb.f. in having a well developed callus at the base of the lip and somewhat smaller flowers. *Telipogon Wallisii* Rchb.f. is very similar to this new species, but its flowers are smaller and its petals are only 7-nerved.

Ecuador: Santa Rosa. 11,000 ft. alt. June 1956. *H. Teuscher 12* (Type in Herb. Ames).

TWO ADDITIONS TO THE ORCHID FLORA OF VENEZUELA

BY
CHARLES SCHWEINFURTH

DURING the course of my investigations on the orchid flora of the Guiana Highlands with special emphasis on Venezuela, the following two species which seem to be amply distinct were discovered.

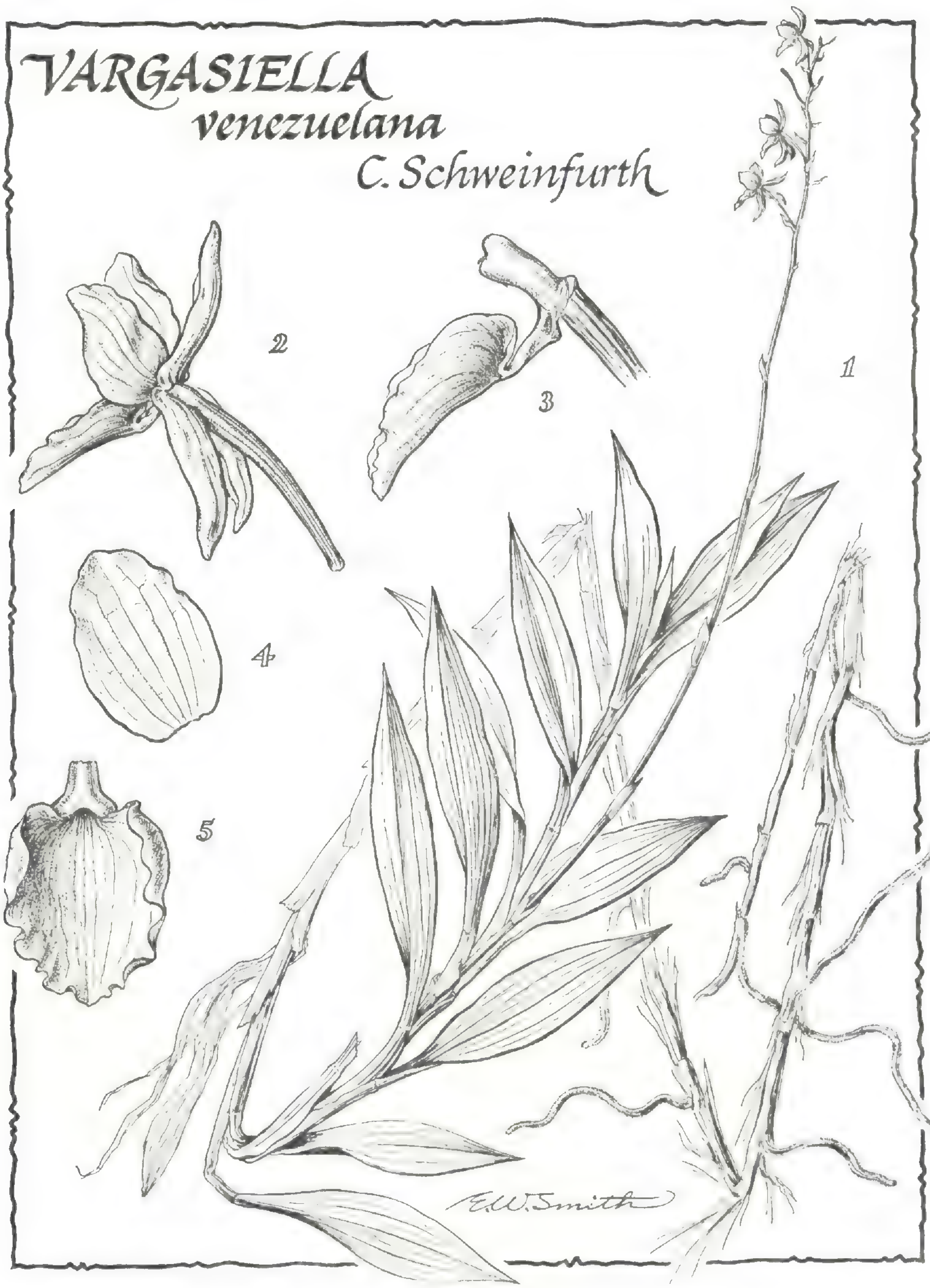
Vargasiella venezuelana *C. Schweinfurth sp. nov.*

Herba terrestris, elata, robusta, in parte inferiore decumbens. Caulis vaginis numerosis, adpressis, imbricantibus, foliiferis omnino celatus. Folia elliptica vel elliptico-oblonga, valde acuminata, ad basim articulatam longe attenuata, submembranacea, plicata. Inflorescentia e folii medii axilla exoriens, elata; pedunculus vaginis nonnullis brevibus, tubulatis remote ornatus; racemus perlaxe pauciflorus. Flores mediocres, laete purpurei, subcrassi, cum sepalis longitudinaliter concavis. Sepalum dorsale expansum lanceolato-oblongum, obtusum vel acutum. Sepala lateralia valde similia sed paullo majora, obliqua. Petala sepalis multo breviora et latiora, ovalia vel oblongo-elliptica, obtusa vel subacuta. Labellum simplex, unguiculatum; unguis brevis sed distinctus, a basi oblonga abrupte dilatatus, carina mediana crassa, apice divisa ornatus: lamina leviter recurva, triangulari-ovata, apice rotundata, basi prominenter cordata. Columna crassa, brevis.

EXPLANATION OF THE ILLUSTRATION

PLATE XLIV. VARGASIELLA VENEZUELANA *C. Schweinf.*
1, plant, one fourth natural size. 2, flower from side, natural position, one and one third times natural size. 3, lip and column from side, natural position, twice natural size. 4, petal, twice natural size. 5, lip, natural position, twice natural size.

Drawn by ELMER W. SMITH


VARGASIELLA
venezuelana
C. Schweinfurth
1
2
3
4
5
E.W. Smith

Plant terrestrial, tall and robust, with a decumbent, sparsely rooting stem, up to about 187.5 cm. long including the erect inflorescence. Roots very remote, solitary, fibrous, rather stout, finely pubescent. Stem entirely concealed by appressed, imbricating, evanescent, leaf-bearing, tubular sheaths of which the lower ones are scarious and disintegrating into fibres and the middle and upper ones are green and leaf-bearing. Leaves elliptic or elliptic-oblong, acuminate to a sharp point, long-narrowed below to an articulated base, submembranaceous, plicate, with five to seven prominent nerves, about 14–17 cm. long, up to 3.3 cm. wide. Inflorescence springing from the axil of one of the middle leaves, up to 52 cm. high; peduncle dull lavender, glabrous, about 43 cm. or less long, remotely provided with about six short, tubular, acute sheaths; raceme very loosely few- (about 9-) flowered, the rachis about 9 cm. or less long. Floral bracts small, narrowly lanceolate, concave, equaling about half of the pedicellate ovary which is up to 2.3 cm. long. Flowers rich purple, subfleshy, with the sepals projecting backward and the petals erect. Sepals longitudinally concave. Dorsal sepal when expanded lanceolate-oblong, obtuse or acute, about 1.5 cm. long and 4.4 mm. wide. Lateral sepals similar, obliquely lanceolate-oblong, obtuse or acute, about 1.6 cm. long and 6 mm. wide. Petals distinctly shorter and broader than the sepals, oval to oblong-elliptic, obtuse to subacute, somewhat concave, up to 1.2 cm. long and 7 mm. wide, the margins often somewhat irregular. Lip simple, clawed, with involute, undulate margins; claw short but distinct, abruptly dilated from an oblong base, about 3 mm. long, provided with a central fleshy keel that divides abruptly into two diverging branches; lamina gently recurved, triangular-ovate, rounded at the apex when expanded, conspicuously cordate at the base, about 1.1 cm. long in the cen-

ter and up to 1 cm. wide; disc fleshy-thickened in the middle below. Column stout, about 5 mm. high.

This plant is the second species referable to the remarkable South American genus Vargasiella. It is clearly distinct from *V. peruviana* C. Schweinf. in its greater vegetative proportions, its bright purple (rather than whitish pink) flowers, its narrower, longitudinally concave sepals and its distinctly clawed lip.

Venezuela: State of Bolívar, Chimantá Massif, northwestern part of summit of Abácapa-tepuí, at 2125–2300 meters altitude, in *Bonnetia* forest, April 13, 1953, *Julian A. Steyermark 74914* (Type in Herb. Ames No. 69272).

Oncidium vagans *C. Schweinf. sp. nov.*

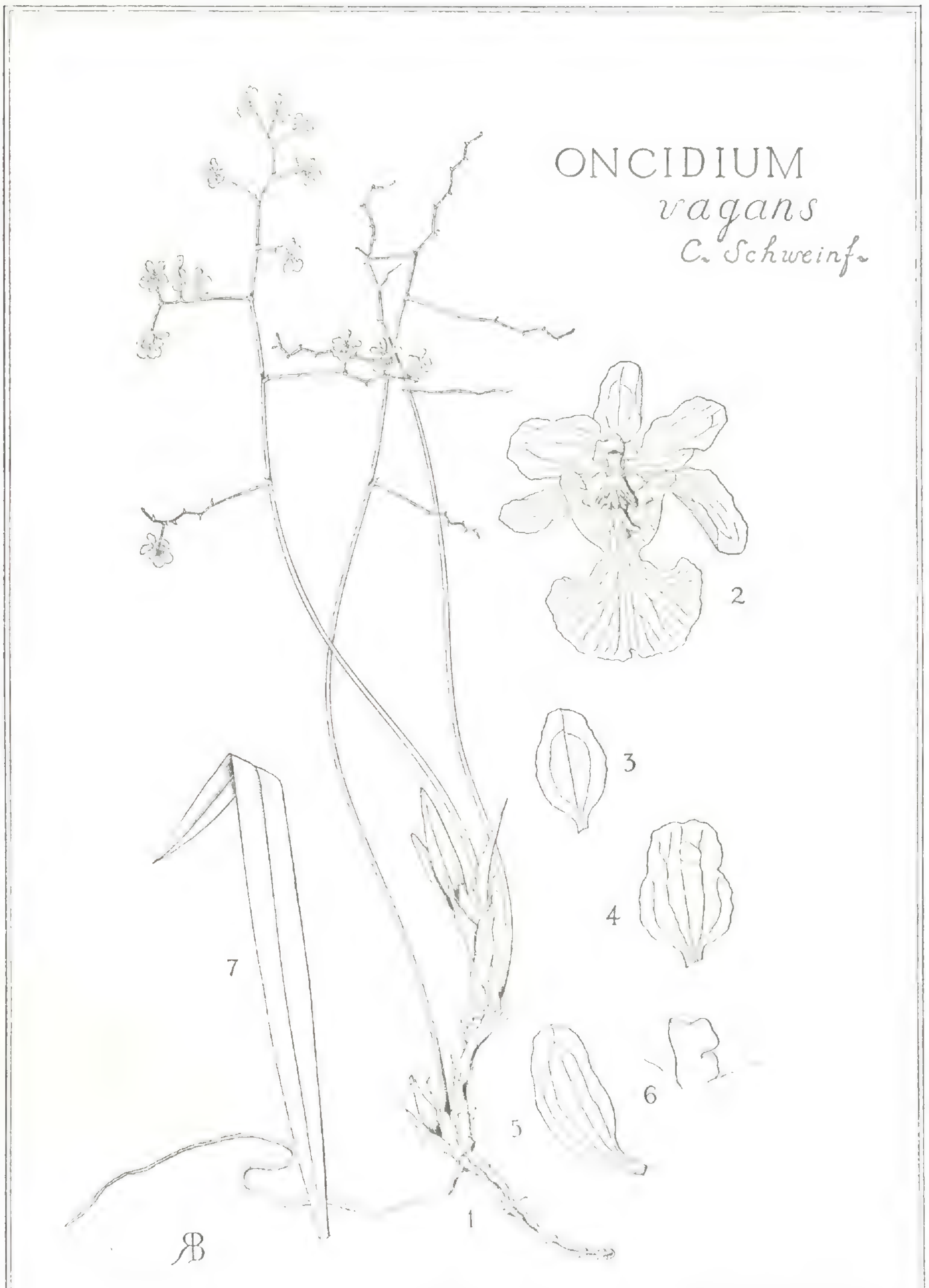
Herba magna, vagans, terrestris vel scandens, valde variabilis. Rhizoma cauliforme, plusminusve crassum, simplex vel in nodo ramosum, vaginis arctis, tubularibus, scariosis, evanidis omnino celatum, radices remotas, simplices, longas nunc emittens. Pseudobulbi remoti, cylindracei vel anguste pyriformes, prope apicem saepissime bifoliati, vaginis nonnullis, scariosis, evanidis inferne ornati. Folia lanceolata vel anguste oblongo-lanceolata vel anguste elliptico-lanceolata, acuta et apiculata, papyracea. Inflorescentia folia multo superans, e pseudobulbi basi exoriens, superne perlaxe paniculata, suberecta; pedunculus vaginis nonnullis, parvis, arctis ornatus; rhachis plusminusve fractiflexa, cum ramis horizontalibus vel decurvis laxe paucifloris. Flores parvi, cum segmentis late patentibus. Sepalum dorsale perbreviter unguiculatum, oblongo-ovatum vel oblongo-ovale, acutum vel apice rotundatum, trinervium. Sepala lateralia oblique obovato-oblonga vel oblongo-oblanceolata, apice rotundata vel acuta, quadrinervia, ad basim paululo unguiculatam angustata. Petala breviter unguiculata, abrupte ovato-oblonga vel oblongo-ovalia, apice lato plusminusve retusa et saepe subacuta, quinquenervia. Labellum segmentis

EXPLANATION OF THE ILLUSTRATION

PLATE XLV. ONCIDIUM VAGANS *C. Schweinf.* 1, plant, one fourth natural size. 2, flower, natural position (lip expanded), twice natural size. 3, dorsal sepal, two and one half times natural size. 4, petal, about twice natural size. 5, lateral sepal, twice natural size. 6, column, from side, three times natural size. 7, leaf (of another collection), approximately one half natural size.

Drawn by RUTH BARTON

Plate XLV



ceteris multo majus, panduratum vel trilobatum; lobi laterales semiovato-triangulares cum angulis exterioribus late rotundatis; lobus anterior reniformi-flabelliformis, apice latissime rotundato emarginatus; discus callo biseriato, basi cuneato, crasse pluridentato ornatus, cum parte apicali conspicue tridentata. Columna parva, cum alis latis, subquadratis superne ornata et crassificatione divaricatim bilobata inferne praedita.

Plant large, sprawling, very variable, terrestrial or climbing. Rhizome stem-like, more or less stout, simple or virgately branched at one of the nodes, entirely concealed by close, tubular, scarious, evanescent sheaths, occasionally producing at remote intervals long, simple, fibrous roots. Pseudobulbs about 3–13 cm. apart, cylindric to narrowly pyriform, commonly 2- (rarely 3-) leaved near the summit, about 2–6.4 cm. long, provided below with several narrow, scarious, evanescent sheaths of which one is produced into an oblong-lanceolate blade. Leaves lanceolate to narrowly oblong-lanceolate or narrowly elliptic-lanceolate, acute and apiculate, papyraceous, 4–14.6 cm. long, up to 1.6 cm. wide. Inflorescences much surpassing the leaves, arising from the base of the pseudobulb, very loosely paniculate above, about 44.5–117.5 cm. long, suberect, often diffuse above; peduncle provided with several remote, small, inconspicuous sheaths, up to 73.5 cm. long; rachis more or less fractiflex with the horizontal or decurved branches loosely 3- to 7-flowered above. Flowers small, with widespreading segments, pale greenish or cream-colored to pale yellow with irregular brownish or purple bands. Dorsal sepal shortly and narrowly clawed, oblong-ovate or oblong-oval, acute to rounded at the apex, 3-nerved, about 6–6.8 mm. long and 3.2–4.5 mm. wide. Lateral sepals obliquely obovate-oblong or oblong-oblanceolate, rounded to acute at the apex, 4-nerved, narrowed to an indistinctly clawed base,

about 8–11 mm. long and 3–4 mm. wide. Petals from a short claw rather abruptly ovate-oblong or oblong-oval, more or less retuse and often subacute at the broad apex, often slightly narrowed or indented on each side, about 6.3–9 mm. long and 4–6 mm. wide, indistinctly 5-nerved. Lip much larger than the other segments, pandurate or 3-lobed, white to cream-colored with purple spots and a yellow callus, about 11–13 mm. in greatest length, about 8–8.7 mm. wide across the basal portion; lateral (basal) lobes semiovate-triangular, broadly rounded at the outer angles, with a more or less distinct, semiorbicular lobule on each side of the base; anterior lobe reniform-flabellate, emarginate at the broadly rounded apex, about 10–11.5 mm. wide; disc with a prominent callus below consisting of two series of which the lower one is cuneate at the base and composed of several small, fleshy teeth and the anterior one of three larger, fleshy teeth; on either side of the callus there is sometimes (as in the type) a single fleshy tooth. Column small, about 3.5 mm. high, with a pair of broad, porrect, subquadrate wings above and a fleshy, divaricately bilobed thickening below.

Oncidium vagans appears to be allied to the Brazilian *O. Warmingii* Reichb.f., but differs in having entire, differently shaped lateral lobes of the lip, sessile mid-lobe and subquadrate column-wings.

VENEZUELA: Bolívar, Central Section, Chimantá Massif, 2120 meters alt., swampy depression in wet savanna along east branch of headwaters of Río Tirica, February 12, 1955, "lvs coriaceous, olive; pseudobulbs subterete. Peduncle reddish brown; lip white to cream with purple spots in center and at apex; callosity yellow with purplish spots; lateral lip appendages white; column purplish above, within whitish with greenish yellow at base; sepals and two lateral petals pale yellow to cream with broad irregular purple bands, locally frequent around hammocks," *Julian A. Steyermark & John J. Wurdack 762* (TYPE in Herb. Ames 68534.—Amazonas, Cerro Duida, Río Cunucunuma (Culebra Creek drainage), 1600 meters alt., "terrestrial; outer perianth members pale greenish, pale brown mottled; lip white with mot-

tled appendages and yellow protuberance. In interzone between Bonnetia and cloud forests," November 19, 1950, *Bassett Maguire, R.S. Cowan & John J. Wurdack 29553*.—Bolívar (The Phelps Uaipán-Tepuí Expedition), at the summit, 1700 meters alt., flowers white, January 25, 1948, *Kathleen D. Phelps & Charles B. Hitchcock 358*.—Bolívar, 1800 meters alt., "semitrepadora o erguida en formación arbustiva baja. Parte central del plató de Auyantepuí, lugar soleado y seco," April 1956, *Vareschi & Foldats 4933*.—Same date as the last, *Foldats 2599*.—Cerro Auyantepuí, at the summit, Alto Caroní, 2100 meters alt., January 1949, *F. Cardona 2743, 2744*.

A LITTLE-KNOWN CULTIVATED PLANT FROM NORTHERN SOUTH AMERICA

BY

RICHARD EVANS SCHULTES

IT is not often that an important economic plant, cultivated over a wide area, hides out from the eyes of plant-explorers, anthropologists, missionaries and travellers—even in an area with such a poorly understood agriculture as the Amazon Valley. Yet that has apparently come to pass in the case of *Solanum Topiro* HBK.

I

During my travels in the northwestern part of the Amazon basin, principally in Colombian territory, it was my custom always to study the plants cultivated by the Indian inhabitants of the region.

It is possible, in general, to arrange the plants which the natives of this tropical forest-region grow into two large categories on the basis of the manner in which they are cultivated. Native agriculture in the western Amazon has been called, and I think perhaps erroneously, "primitive." Whether or not it be primitive, it is true that no machinery is employed, and little or no formal planning underlies agricultural practices. Plants are either set out in fields devoted to a single crop or else they are put in or allowed to spring up individually at random mingled with several or many different species.

The first of these two categories can claim, at least, in the northwestern part of the vast Amazon, only two species: *yuca* (*Manihot esculenta* Crantz) and *coca* (*Erythroxylon Coca* Lam.). All other cultigens grow singly

or in groups of several individuals scattered through fields of yuca or coca, along the edges of these fields, in clearings or close to house-sites. Many species of economic plants fall into this second category. We might cite, as a few examples, the following: *Phyllanthus* spp., *Tephrosia toxicaria* Pers. and *Clibadium asperum* (Aubl.) DC. (fish-poisons); *Nicotiana Tabacum* L. and *Banisteriopsis* spp. (narcotics); *Capsicum frutescens* L. (spice); and *Herrania nitida* (Poepp.) R. E. Schult. (food).

In wellnigh every Indian agricultural plot in the Colombian Amazonia, especially along their margins and in the immediate vicinity of dwellings, two shrubby species of *Solanum* are grown for their edible fruits. The more abundant of these has been determined as *Solanum Topiro*. We have still not been able satisfactorily to identify the second, and, common though it be in the areas of Indian agriculture, it may well represent a concept hitherto undescribed. The present paper, however, treats only of *Solanum Topiro*.

It is with pleasure that I acknowledge the very helpful interest of Mr. and Mrs. Kendal Morton of the Morton Collectanea (University of Miami) in my attempts to identify specimens of this plant which I had brought back from Colombia. I have also here to thank Mr. Elmer W. Smith, artist at the Botanical Museum of Harvard University, who has seen *Solano Topiro* in its native state in garden-plots in the Colombian Vaupés, for his outstanding drawing which was made possible through a grant from the National Science Foundation. This is the first time that *Solanum Topiro* has been illustrated.

II

It may be well to outline what little we know of the history and recent introduction into horticulture of this species.

A scrutiny of the major works on tropical fruit plants indicates that *Solanum Topiro* has been completely neglected and probably unknown as a cultigen. It does not, for example, appear in Wilson Popenoe's "Manual of tropical and subtropical fruits" (1920), in F. C. Hoehne's "Frutas indígenas" (1946) nor in Adolfo Ducke's "Plantas da cultura precolombiana na Amazônia brasileira. . ." in Bol. Téen. Instit. Agron. Norte, no. 8 (1946). Furthermore, standard anthropological and botanical papers on Indian agriculture in the American tropics fail to mention it: Robert H. Lowie, "The tropical forests: an introduction" and Carl O. Sauer, "Cultivated plants of South and Central America" in Handbook of South American Indians [ed. J. H. Steward], Bur. Am. Ethnol. Bull. 143, 3 (1948) 2 and 6 (1950) 487, respectively. As Fennell (Fennell, Joseph L. "*Cocona* – a desirable new fruit" in For. Agric. 12 (1948) 181) has written: "To what extent, if any, the *cocona* [*Solano Topiro*] may have reached the gardens of the outside world is difficult to say. That it appears even now to be essentially unknown to horticulture leads me to believe, in light of its impressive appearance and apparent usefulness, that it may never have previously left its secluded habitat as a recognized fruit of value."

So far as I have been able to ascertain, the first serious attention paid by botanists to *Solano Topiro* as a cultigen dates from the middle of the 1940's. During this period, seeds of the plant were collected "from the little-explored reaches of the upper Amazon" (presumably in Peru) and established in the Experiment Station at Tingo María in Peru. Eventually, it was introduced to the Instituto Interamericano de Agricultura Tropical in Turrialba, Costa Rica (Fennell, loc. cit.; Ochse, J. J. "*Solanum hyporhodium* or *cocona*" in Proc. Fla. State Hort. Soc. 66 (1953) 211) from which centre it began to attract horticultural attention.

The vernacular name for *Solanum Topiro* in Peru is reported to be *cocona*. This is borne out by notes on herbarium specimens (*Killip & Smith 27367, 27323*) collected in the Amazonian part of Peru in 1929. This convenient epithet followed the plant in its several introductions and has now, in the literature, been accepted as a standard common name. Unfortunately, however, *cocona* has been erroneously identified and has, in agricultural institutions as well as in the scientific and popular literature (Fennell, loc. cit.; "Cocona" (abstract of foregoing article) in Econ. Bot. 3 (1949) 216; Ochse, loc. cit.; [Bischoff, William] "The Peach Tomato" in Miami Daily News (March 7, 1954)) been determined as *Solanum hyporhodium* A. Br. et Bouché.

It has not been possible for me to ascertain where this erroneous identification was made, nor do I find in any of our larger herbaria a specimen-voucher upon which it could have been based. In the card-file at the Subtropical Experiment Station in Homestead, Florida, the following data relative to *cocona* are to be found: "*Solanum hyporhodium* A. Br. & Bouché. Native to Australia. In 1948, seeds were received from F. B. Harrington, Natal: all plants dead by 1950 from nematodes."

That there must have been a sudden and widespread distribution of seeds of this species is evidenced by the fact that the Subtropical Experiment Station, believing the plant to be native to the Old World, made an introduction from South Africa. Ochse (loc. cit.) brought the species into cultivation at the University of Miami apparently directly from Costa Rica. In July, 1958, I found it growing experimentally at the Imperial College of Tropical Agriculture in Trinidad, the result of a relatively recent introduction but with no record of the provenience of the seed.

Identification of the material of *Solanum Topiro* which

I had gathered in the northwest Amazon puzzled me for a number of years. I was finally able to match my material collected in Colombia under the name *lulo* with *cocona* through illustrations of *cocona* found in the Morton Collectanea and to learn that *cocona* had been determined as *Solanum hyporhodium*. In trying to check the accuracy of this determination, I discovered that there was no material representative of *Solanum hyporhodium* in our American herbaria. The type, and, apparently the only specimen of this species, was preserved in the Berlin Herbarium and, of course, is no longer extant. There is, nevertheless, a photograph of the type of *Solanum hyporhodium* in the Gray Herbarium. It is at once obvious that *cocona* cannot be referred to *Solanum hyporhodium*, for the photograph indicates that there are differences in the leaf and that *S. hyporhodium* has stems and petioles which are heavily spinose. The cocona collected originally in Peru, as well as all of my own specimens from Colombia and recent Venezuelan material, is entirely without spines and has the petioles clad with a soft mottled indumentum. Fennell's published notes (loc. cit.), indeed, stress the lack of spines.

It was possible for me finally to identify *cocona* or *lulo* by using one of the common Venezuelan names of the species. The non-Indian population of the Colombian Amazonia know the plant as *lulo*, because of its strong resemblance to the highland *Solanum quitoense* Lam., which, in the Andes of Colombia, is called *lulo*. Along the border between Colombia and Venezuela, however, the non-Indian inhabitants refer to the plant by its Venezuelan name *topiro* or *tupirú*. In H. Pittier's "Manual de las plantas usuales de Venezuela" (1926) 385, there is an entry under the common name *topiro:* "*Solanum Topiro* Dunal, Synops. 10. 1810. Sin. *tupiro*. Especie herbácea, tomentosa, inerme, las hojas ovales, más o

menos angulosas, las flores verduscas en glomérulos opuestos a las últimas y los frutos ovoideos, grandes y comestibles. Es del Alto Orinoco." Sturtevant ("Sturtevant's notes on edible plants" [ed. U. P. Hedrick], (1919) 545) had reported *Solanum Topiro*, a species growing on the "banks of the Orinoco," as having an edible fruit known as the "turkey berry," attributing his sources to G. Don Hist. Dichl. Pls. 4 (1838) 410.

An excellent photograph of the type of *Solanum Topiro* from the Paris Herbarium enabled me to authenticate the identification. The type, from the Humboldt and Bonpland Herbarium, was collected at San Fernando de Atabapo on the Río Orinoco, Venezuela (*Humboldt et Bonpland 918*). There is, further, in Paris a reproduction of an unpublished drawing of *Solanum Topiro* (No. 192) for Dunal's Solanaceae, ed. 2. There can be no doubt that *cocona* from Peru and the *lulo* from Amazonian Colombia refer to the same species as *topiro* in Venezuela and that all three are *Solanum Topiro*. We are now able to offer an amplified description and extended distribution for this species, as well as sundry ethnobotanical notes appertaining to its cultivation and use.

Solanum Topiro *Humboldt, Bonpland & Kunth ex Dunal* Sol. gen. aff. syn. (1816) 10.

ORIGINAL DESCRIPTION:

37. S. Topiro. S. caule herbaceo tomentoso, foliis ovato-oblongis sinuatis basi inaequalibus subtus leviter tomentosis supra sericeis, floribus aggregatis extra-axillaribus, baccis ovatis.—*Humb. et Bonpl.* ined.—*Dun. Sol. Ed. 2 ined. tab. 921 f. 1* Hab. ad Orenocum (v.s.h. H. et B.).

Shrub unarmed, robust, rank, up to about 5 feet (1.5 m.) tall. Branches stout, terete, scurfy-pubescent, grey-green in life. Twigs densely white-stellate-tomentose. Leaves coarsely membranaceous, ovate in outline, at maturity

up to about 48 cm. long, 36 cm. wide, basally inequilaterally truncate, apically abruptly acute, marginally very distantly and very deeply sinuate, strongly petiolate (petiole up to 12 cm. long, densely white-stellate-tomentose); upper surface coarsely tomentose and densely clad with somewhat stiff sericeous white hairs (some of which have basally a stellate formation) sparsely interspersed with white stellate hairs; nether surface very softly and densely white-stellate-tomentulose; veins strong and conspicuous above and below, extremely densely white-stellate-tomentose. Inflorescence a lateral, very short-peduncled, few-flowered cyme. Flowers pedicellate; pedicels up to 6 mm. long, 1.5–2 mm. in diameter, very densely stellate-tomentulose. Calyx lobes somewhat crassulent, more or less triangular-ovate, apically subacute, up to about 15 mm. long, very densely and softly greyish brown-stellate-tomentose without, glabrous but with minute white scabs within. Corolla membranaceous, white or greenish white, lobes oblong-ovate, up to about 20 mm. long, apically subacute, glabrous within, densely stellate-tomentulose without. Anthers yellow, erect, linear, about 9–10 mm. long. Style terete, 7–8 mm. long. Ovary globose, very densely long-white-sericeous. Fruit subglobose to ovoid, ripening orange-red, sometimes tomato-red, densely and minutely stellate-tomentulose (hairs easily caducous upon handling), becoming subglabrous upon ripening. Pulp acidulous. Seeds very numerous, flat, oval in outline, 3–4 mm. long, 2–2.5 mm. wide, pale yellowish.

COLOMBIA: Comisaría del Amazonas, Río Caquetá, vicinity of La Pedrera. "Fruit dark red-rust, hairy. Flowers white. Bush." April 1944, *R. E. Schultes 5881*.—Comisaría del Amazonas, Río Loretoyacu. Altitude about 100 m. September 1946, *R. E. Schultes & G. A. Black 8394*.—Comisaría del Amazonas, Río Apaporis, Soratama, near mouth of Río Kananari. "Cultivated. Fruit edible. Flowers whitish with yellow anthers. Fruit ovoid, orange, covered with hair in unripe stage. *Lulo. Tupirú.*" March 1951, *R. E. Schultes 12081*.—Comisaría del

EXPLANATION OF THE ILLUSTRATION

PLATE XLVI. SOLANUM TOPIRO *HBK*. 1, flowering branch, with medium-sized leaf, about one half natural size. 2, portion of the upper surface of the leaf, greatly enlarged. 3, portion of the nether surface of the leaf, greatly enlarged. 4, inflorescence, about one half natural size. 5, fruits, about one half natural size. 6, young leaf, about one half natural size.

SOLANUM
Topiro
HBK.
2
3
6
1
4
5

EXPLANATION OF THE ILLUSTRATION

PLATE XLVII. Fruit of SOLANUM TOPIRO represented by the collection *Schultes 12081* from the Colombian Amazonas.

Photograph by RICHARD EVANS SCHULTES

Plate XLVII

EXPLANATION OF THE ILLUSTRATION

PLATE XLVIII. Habit photograph of SOLANUM TOPIRO represented by the collection *Schultes 12081* from the Colombian Amazonas.

Photograph by RICHARD EVANS SCHULTES

Plate XLVIII

Amazonas, Río Apaporis, Soratama, between Río Pacoa and Río Kananarí. Altitude about 250 m. "Flowers greenish. Anthers yellow. Bush. Fruit green, turning orange. Kubeo = *be-tá-ka;* Taiwano = *de-twá;* Tatuya = *de-twá.* Cultivated." September 1, 1951, *R. E. Schultes & I. Cabrera 13842.*—Comisaría del Vaupés, Río Vaupés, Mitú. "Flowers yellow-green. Fruit edible." June 22, 1958, *H. García-Barriga, R. E. Schultes & H. Blohm 15771.*

PERU: Departamento de Junín, Puerto Yessup. Altitude about 400 m. "Coarse, erect herb 2–3 ft. Corolla light green, anther yellow. July 10–12, 1929, *E. P. Killip & A. C. Smith 26363.*—Departamento del Loreto, Iquitos. Altitude about 100 m. "Local name *cocona.* Coarse herb 3–5 ft. Corolla greenish white. Anthers yellow. Fruit light red, edible. Clearing." August 2–8, 1929, *E. P. Killip & A. C. Smith 27367.*—Departamento del Loreto, Yurimaguas, lower Río Huallaga. Altitude about 135 m. "Coarse herb, 3–4 ft. tall. Corolla greenish white. Anthers yellow. Clearing." *E. P. Killip & A. C. Smith 27999.*—Departamento del Loreto, Puerto Arturo, lower Río Huallaga, below Yurimaguas. Altitude about 135 m. "*Cocona.* Fruit edible. Coarse herb 2–4 ft. Corolla green; fruit red. Clearing." August 24–25, 1929, *E. P. Killip & A. C. Smith 57823.*

VENEZUELA: Territorio del Amazonas, Río Orinoco, San Fernando de Atabapo. *A. Humboldt & Bonpland 918.*—State of Bolivar, lower portion of Quebrada Oparu-ma, tributary of Río Pacairao, below Santa Teresita de Kavanayen. Altitude 915–1065 m. "Camarata Indian name: *bo-pó.* In conuco. Herb 2 feet tall. Leaves membranaceous, rich grass-green above, grey-green below. Fruit yellow, edible, made into preserves." November 25, 1944, *J. Steyermark 60531.*

Solanum Topiro has never apparently been collected from the wild and, in more than twelve years in the northwest Amazon, I have never seen it outside of agricultural plots or abandoned house-sites which obviously had been the scene of cultivation. I believe that we have at hand in this plant a species so long in association with man that it may nowadays exist only because of this association. The fruit yields viable seeds in great abundance, but the plants seem to reproduce themselves only in highly disturbed and sunny sites.

The Indians eat the ripe fruit as a tomato. The civilized inhabitants of the region use the fresh fruits to prepare, with sugar, a rather acidulous, thirst-quenching drink. To my knowledge, the plant is never set out de-

Plate XLIX

Plate XLIX. Flowering branch of Solanum Topiro.

Photograph by Richard Evans Schultes

liberately but springs up from seeds adhering to the rind when this is cast into refuse heaps or when inedible parts of the fruit are spat out in the process of eating. The species is grown over a wide area which includes much of forested eastern Peru, most of the Amazon drainage-area of Colombia, the upper reaches of the Orinoco system in Venezuela and probably adjacent parts of Brazil. I have never encountered it in Brazil, however, but it may be grown there on a much reduced scale because of the sparsity in the westernmost Amazon of Brazil of unacculturated Indian tribes.

The type and flavor of the fruit and the heavy bearing characteristics of *Solanum Topiro* make the plant rather promising as a new subtropical fruit-crop, especially to residents in Florida. As Fennell wrote (loc. cit.): "As an economic commodity, from the long-range viewpoint, obviously the cocona offers much in the way of improvement potential. The complementary values afforded by the various closely related species of this section of the genus are not commonly available to most crop-improvement projects. It now remains for us to devise a way to blend and proportion these values satisfactorily toward developing the end product of superior hybrid combinations." In any crop-improvement program, the value of having living material of this rather variable species from all or many parts of its range should not be overlooked. Since Ochse's notes (loc. cit.) in 1958, apparently nothing has appeared which would point to further horticultural work in Florida with *Solanum Topiro*. At that time, Ochse pointed out that nematodes were an important enemy of the plant. The situation is well summarized, I believe, by Fennell (loc. cit.) when he states that ". . . a safe assumption is that even in its present unimproved state the cocona is a permanent acquisition as a valuable horticultural plant."

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NEW CONSIDERATIONS IN AN OLD GENUS: *DATURA*

BY

ARTHUR S. BARCLAY

THE genus *Datura* has received considerable attention over the years from ethnobotanists and pharmacologists whose interest in this group of plants stems from the presence of the toxic alkaloids contained in most, if not all, of the species. The herbaceous members of the genus have assumed an outstanding position in the annals of experimental botany at the hands of geneticists and cytologists. In spite of the amount of space devoted to this genus in the literature, we are still in need of an adequate taxonomic treatment. It is hoped that this paper will help to clarify some of the nomenclatorial intricacies surrounding two species well known to botanists and workers in allied fields. Furthermore, descriptions of three new species which were discovered during the preparation of a monograph of the genus are included.

There has been much controversy concerning the correct name for the species which has been known as *Datura meteloides* DC. ex Dunal, but which preferably should be called *D. inoxia* Miller. In order to understand how this confusion came about it is necessary to present a brief résumé of the nomenclatorial history of these concepts.

I. The Typification of *Datura meteloides* DC. ex Dunal

The name *Datura meteloides* was first proposed by Dunal in a manuscript which he sent to Alphonse de Candolle, who in turn published the epithet in his Prodromus (1852). Hence, the correct citation should be *Datura meteloides* DC. ex Dunal. Alphonse de Candolle based his concept of *D. meteloides* on both the drawing and the description by Sessé and Mociño as we may see from the following note in the Prodromus: "In calidis Novae Hispaniae regionibus. D. Metel Moc. et Sess. pl. Mexic. ined. ic. et mss. t. 919, collect. transl. Candoll." The original Sessé and Mociño illustrations were loaned to August Pyramus de Candolle and were recalled on short notice. As a result, de Candolle, who recognized the value of these drawings, enlisted the help of the townspeople of Geneva to make copies of them before sending them back. One of these copies, Icones no. 919, has served as the type of *D. meteloides* and is now preserved in the Candollean Herbarium (Ewan, 1944).

In 1855, a new *Datura* was brought into cultivation by the French horticulturist M. Louis Vilmorin from seeds sent him by Asa Gray who had obtained them from a collection made by Charles Wright (no. 526) in western Texas in 1849. This plant was cultivated and distributed under the name of *Datura meteloides* (Ewan, 1944). M. Ortgies, an employee of the Vilmorin Co. of France, noticed the discrepancy between de Candolle's description of *D. meteloides* and the plant cultivated under the same name and brought it to the attention of the German botanist, Dr. Eduard von Regel. As a result, a new species, *D. Wrightii*, was published by Regel (1859).

Gray (1878) considered the southwestern perennial species of the United States to represent *Datura mete-*

loides and relegated *D. Wrightii* to synonymy handling the obvious lack of agreement between the two descriptions with the following comment: ". . . Dunal in DC. Prodr. l.c. 544 (the descr. and drawing of Mocino and Sesse wrong as to 10-dentate corolla)." This erroneous interpretation was adopted by Safford (1921) who apparently followed Gray.

It is obvious from Dunal's monograph (1852) that he had no knowledge of *Datura inoxia* Mill. (Miller, 1786) which, since it is apparently identical with *D. meteloides*, enjoys priority. Miss Helen Timmerman (1927), although recognizing the problem existing in the literature, failed to reach a satisfactory conclusion regarding *D. meteloides* and *D. inoxia* probably due to insufficient material at hand.

Recently, Ewan (1944) became cognizant of the problem concerning the discrepancy between the description of *Datura meteloides* sensu DC. and our perennial southwestern species commonly known by that name. In attempting to unravel this confusion he presented an excellent account of the historical backgrounds of both *D. meteloides* and *D. Wrightii*. His conclusion that de Candolle's *D. meteloides* "cannot be shown to be a misapplied binomial because no other species of *Datura* has been found in central Mexico which agrees with the original description nor the drawing upon which it is based" is hardly acceptable due to the ample herbarium material of *D. inoxia* at hand. Furthermore, his recommendation that the name to be applied to our perennial species should be *D. Wrightii*, provided the identity of *D. meteloides* DC. ex Dunal cannot be ascertained, requires more thought. His proposal that the collection *C. Wright no. 526* (US 60042) be designated as lectotype of *D. Wrightii* with Turkey Creek, Uvalde-Kinney Co. line, Texas as type locality appears to be a wise choice, but,

EXPLANATION OF THE ILLUSTRATION

PLATE L. The illustration of DATURA METELOIDES *DC. ex Dunal* in the Candollean Herbarium which formerly served as type.

Plate L

EXPLANATION OF THE ILLUSTRATION

PLATE LI. Isotype of DATURA METELOIDES preserved in the Chicago Natural History Museum.

Photograph by A. S. BARCLAY AND R. T. MOORE

Plate LI

847215
HERBARIUM HORTI BOTANICI MATRITENSIS
Plantae Novae Hispaniae.
a Sessé, Mociño, Castillo et Maldonado lectae
(1787-1795-1804).
Datura innoxia Mill.
"Datura Metel N."
n. 1572

EXPLANATION OF THE ILLUSTRATION

PLATE LII. Neotype of DATURA INOXIA *Miller* preserved in the British Museum.

Photograph sent by J. E. DANDY

Plate LII

CULTIVATED PLANTS
Datura innoxia Miller
Cultivated at: Chelsea Physic Garden

1843

Stramonium Americanum
maximum, flore albo,
fructu rotundo spinoso

1758.

Specimen listed in Phil. Trans 51. 99 no. 1843 (1760) as one of the 'Fifty Plants from Chelsea Garden presented to the Royal Society by the worshipful Company of Apothecaries for the Year 1757, pursuant to the Direction of Sir Hans Sloane'

T8
1958

according to the present provisions of the International Code of Botanical Nomenclature (Art. 7, Note 3, 1956), *C. Wright no. 526* should be considered a neotype rather than a lectotype as suggested also by Fosberg in a personal communication to me.

Fortunately, I have seen a specimen from the Chicago Natural History Museum which was collected by Sessé and Mociño and labeled by them as "Datura Metel N." Excepting for the fruit, this specimen is identical with the illustration of *Datura meteloides* DC. (see Plates). Because of this outstanding similarity and since there is no other specimen which could fit the needs, I believe that this must represent the type collection. Inasmuch as the Chicago specimen consists of flowering material only, it seems probable that the fruits in the illustration represent an incorrect addition by an unknown artist. However, I have not yet seen the specimen in the Madrid Herbarium (MA). The Sessé and Mociño specimen mentioned above is a duplicate of the original collection. Therefore, the material in the Madrid Herbarium should serve as type specimen, and the Chicago material, *Sessé, Mociño, Castillo et Maldonado, No. 1572* ! (F no. 847215) as an isotype. *Datura meteloides*, as typified above, is identical with the earlier *D. inoxia* of which it is therefore, a synonym. It is, furthermore, distinct from *D. Wrightii*.

II. The Typification of *Datura inoxia* Miller

Datura inoxia was described by Philip Miller (1768) from plants grown from seed which he had received from "La Vera Cruz." No type specimen was designated at that time, but there are specimens in the British Museum which were cultivated at the Chelsea Physic Garden during Miller's curatorship (1722-1770). In the absence of a type specimen, one of these may serve.

The Chelsea Physic Garden, according to Dandy (1958), "was conveyed in 1722 to the Society of Apothecaries by Sloane (who had purchased the manor of Chelsea in 1712) on certain conditions, one of which was the 'rendering yearly to the President, Council and Fellows of the Royal Society of London, fifty specimens of distinct plants, well dried and preserved, which grew in their garden the same year, with their names or reputed names; and those presented in each year to be specifically different from every former year until the number of two thousand shall have been delivered'." This stipulation resulted in the accumulation of an herbarium of over 3000 specimens taken from the Sloane estate. The lists of plants so prepared were printed annually in the Philosophical Transactions (of the Royal Society) from 1723 to 1774. In 1781, the specimens were transferred to the British Museum and are now incorporated in the general herbarium.

Miller described the Chelsea plants in successive editions of his Gardener's Dictionary and as Stearn communicates, "when there is no specimen extant from Miller's own herbarium. . . . the application of a Miller name can often be determined or checked by a contemporary specimen from the Chelsea Garden, even though such a specimen was not dried and labelled by Miller himself."

There are, in my possession, excellent photographs of two authentic specimens of *Datura inoxia* cultivated at the Chelsea Garden and kindly sent by J. E. Dandy of the British Museum. Having examined these, I hereby designate as neotype the specimen listed in the Philosophical Transactions (of the Royal Society) 51 (1760) 99, no. 1843.

Since *Datura inoxia* and *D. meteloides* are identical, the former binomial which has priority must be taken up for this concept.

III. Descriptions of New Species

Datura kymatocarpa *Barclay sp. nov.*

Caulibus dichotomis, usque ad 40 cm. altis; foliis in ambitu ovatis, apice acutis, basi inaequalibus, margine irregulariter lobatis vel sinuato-dentatis, usque ad 11 cm. longis, dimidio seu duabus-tertiis partibus latis, utrinque strigosis; floribus erectis, axillaribus; pedicellis per anthesin 0.7–1.8 cm. longis, post anthesin elongatis reflexisque; calyce cylindrico, 2.8–4.6 cm. longo, apice 5-dentato, dentibus triangularibus; corolla albida, infundibuliformi, plicata, 6–7.5 cm. longa, orificio 5-dentato, dentibus acuminatis, 3–4 mm. longis; capsula globosa, irregulariter dehiscenti, setis semicapillaceis satis dense obtecta, 2.4 cm. longa; seminibus reniformibus, testa verrucosa.

Caulescent, dichotomously branching annual herbs, reaching 40 cm. or more in height; young branches usually villous, becoming glabrescent with age; leaves alternate, ovate in outline with an acute apex and an unequal base extended into a villous up to 8 cm. long petiole; margin irregularly lobate or sinuate-dentate; leaf blades up to 11 cm. long and usually one-half to two-thirds as broad, variously strigose on both surfaces except along the mid-vein where it is villous in the same manner as the petiole; pedicellate flowers erect, borne in the axils of the branches; pedicels during anthesis 0.7–1.8 cm. long, later becoming somewhat elongated and reflexed; calyx tube cylindrical, 2.8–4.6 cm. long and sparsely pubescent with a 5-dentate apex, teeth triangular in shape, 3–5 mm. long and 3–5 mm. broad at the base; corolla white, funnel-shaped, plicate, terminating in a 5-dentate orifice, 6–7.5 cm. long; the five corolla teeth acuminate, 3–4 mm. long and 3 mm. wide at the base, each of them supported by three conspicuous nerves, the median one

extending to the tip; the margin between each tooth bisinuate and forming an obtuse lobule giving the corolla the appearance of being 10-angled; the five stamens free, epipetalous, attached to the corolla tube at approximately the same level, about 2.5–3 cm. from the base; filaments glabrous, 2–2.3 cm. long; style equalling or slightly exceeding the anthers, 4.6–5.7 cm. long; young ovary covered with spine-like hairs; calyx circumscissile, shed with the corolla, the persistent base expanding into a membranous disk-like structure subtending the capsule, 1.5–2 cm. in diameter on mature fruit; capsule globose, pubescent, pendent on 1.5–2 cm. long pedicels; irregularly dehiscent, covered with semicapillaceous pubescent bristles, up to 2.4 cm. long; seeds reniform, about 5 mm. long and 3.5 mm. wide, seed coat verrucose.

Mexico: State of Mexico, Dist. of Tamascaltepec, Bejucos, "llano," Aug. 15, 1935, *G. B. Hinton et al 8173* (Type in US 1841574).—State of Guerrero, Dist. of Coyuca, Pungarabato, "roadside," July 9, 1935, *G. B. Hinton et al 8030* (F, MO, US): Rio Balsas, Aug. 26, 1910, *C. R. Orcutt 4384* (F).—State of Michoacan, Municipality of Apatzingan, "open sun-baked pasture one-half mile S. of Apatzingan, thick adobe soil, alt. 1200 ft.", July 31, 1940, *W. C. Leavenworth 409* F, GH, MO, NY); Municipality of Apatzingan, "common between thorn forest and road, between Apatzingan and La Majada, alt. 1200 ft.", Aug. 16, 1941, *W. C. Leavenworth & H. Hoogstraal 1615* (F, GH, MO, NY).

This species is known only from the Rio Balsas valley in Mexico. According to Leopold (1950), this valley is a tropical inland basin, cut off from the sea by highlands on all sides. In this basin, one encounters a nearly insular type of endemism, and an appreciable number of new species have been described from the collections of Hinton and Leavenworth from this general vicinity. This new *Datura* was collected by Leavenworth in the vicinity of Apatzingan at an altitude of 1200 feet and in an area designated by him as open, arid, scrub forest, which

covers the greater part of the plains of the valley-floor (Leavenworth, 1946).

Datura kymatocarpa may be readily distinguished from all other members of the genus by the semi-capillaceous bristles on its fruit and by its very characteristic seeds (see Plates). The specific epithet is derived from the Greek referring to the wavy hairs on the fruit.

Datura reburra *Barclay sp. nov.*

Pars quae adest usque ad 30 cm. alta, caulibus dichotomis, glabris; foliis in ambitu ovato-lanceolatis, apice acutis, basi inaequalibus, margine irregulariter lobato-dentatis, usque ad 8 cm. longis, dimidio vel duabus-tertiis partibus latis, lamina utrinque glaberrima; floribus pedicellatis, axillaribus, primum plusminusve erectis, deinde post anthesin valde nutantibus; calyce prismatico, carinato-angulato, ca. 6 cm. longo, apice 5-dentato, dentibus satis prominentibus, ovato-lanceolatis, 1.7-2 cm. longis; corolla infundibuliformi, plicata, usque ad 9.5 cm. longa, fauce ampla, 5-dentata, dentibus setiformibus, ca. 5 mm. longis; capsula globosa, puberula, regulariter dehiscenti, pendula, spinis rigidis, acuminatissimis ornata, ca. 2 cm. longa; seminibus reniformibus, lacunis luniformibus utrinque donatis.

Dichotomously branching herb at least 30 cm. tall, but surely more (the specimen at hand is incomplete); young branches strigose, becoming glabrous with age, entire plant appearing glabrous except when young; leaves alternate, ovate-lanceolate in outline, with an acute apex and an unequal base extended into a puberulent petiole, up to 4.8 cm. in length; margins irregularly lobate-dentate; leaf blades mostly incomplete in our specimen, up to about 8 cm. or more in length, one-half to two-thirds as broad, surfaces essentially glabrous except for the sparsely strigose veins; erect pedicellate flowers borne

in the axils of the branches; the strigose pedicels during anthesis about 1 cm. long becoming elongated and reflexed with age; prismatic calyx tube 5-toothed at the apex and keeled along the angles, glabrous on both sides, about 6 cm. long; the calyx teeth ovate-lanceolate, 1.7–2 cm. long and 0.5 cm. wide at the base; corolla funnel-shaped, plicate, terminating in a 5-dentate orifice, up to 9.5 cm. long; the five corolla teeth setiform, about 5 mm. long and 2 mm. wide at the base, each of them supported by three conspicuous nerves, the median one extending to the tip; exterior of the corolla tube glabrous, the interior pubescent from the base up to the point where the filaments are attached to the corolla tube, then becoming glabrous above this point; the five stamens free, epipetalous, attached to the corolla tube at approximately the same level about 3 cm. from the base of the corolla; filaments glabrous except near their attachment to the corolla, 2.8 cm. long; anthers about 6 mm. long with filamentous trichomes along the lines of dehiscence; style 7.8 cm. long; calyx circumscissile, forming a reflexed frill, up to 1.3 cm. long, which subtends the fruit; capsule globose, about 2 cm. long, regularly dehiscent by four valves, pendent on pedicels up to 2.2 cm. long; fruits covered with stiff, sharply pointed spines; surface of fruit puberulent, spines glabrous; seeds reniform, about 5 mm. long and 4 mm. broad, with lunate lacunae on the lateral faces and with a triple ridge along the convex edge which forms a cord-like margin around the seed.

Mexico: State of Sinaloa, vicinity of Culicán, Sept. 14, 1904, *T.S. Brandegee s.n.* (Type: UC 103947).

Datura reburra is similar to *D. discolor* Bernh. in having both nodding fruit and regularly dehiscing capsules. It is, however, readily distinguishable by its distinctive seeds, its puberulent fruit with glabrous spines and its

smaller flowers. The specific epithet of *Datura reburra* refers to the bristling hairs of the capsule.

The question arises, in connection with this new species, as to the validity of the sections *Stramonium* Bernh. and *Dutra* Bernh. The *Stramonium*-section has been distinguished by erect and regularly dehiscing capsules; the *Dutra*-section by nodding and irregularly dehiscing capsules. Both *Datura reburra* and *D. discolor* are characterized by having nodding capsules that dehisce regularly by four valves. Thus, they provide intermediates between the two sections in question.

Prior to my discovery of *Datura reburra*, Fosberg had called my attention to the vague distinction between these two sections, pointing out the nonconformity of *D. discolor* to either one. This additional species would tend to support the belief that these two sections are untenable, unless we propose a new section for every second or third species. Such a procedure would be definitely absurd.

In light of the genetic and cytological work on *Datura* already completed by the late Dr. Blakeslee and by his co-workers, a more thoroughgoing study of these new species should prove to be profitable. Experimental approaches further our knowledge of plants and their relationships to a great degree. Nevertheless, much can also be learned from a study of herbarium material. In fact, such a study should logically precede experimental lines of research.

Datura vulcanicola *Barclay sp. nov.*

Planta fruticosa, usque ad 3 m. alta; foliis ovatis vel ovato-ellipticis, apice acutis, basi in petiolum decurrentibus, utrinque puberulescentibus, margine integra vel irregulariter sinuato-dentata; floribus solitariis, plus-minusve horizontaliter cernuis vel nutantibus arcuatis; calyce glabro, paulo inflato, cylindrico, 4.5–8 cm. longo,

apice inaequaliter 2–4 dentato: corolla usque ad 20 cm. longa, urceolata, apice 5-dentata, margine inter dentes breviter retusa; capsula obovata, prominenter bisulcata, irregulariter verrucosa, usque ad 12 cm. longa; semine reniformi, testa glabra; numerus chromosomicus, 2n = 24.

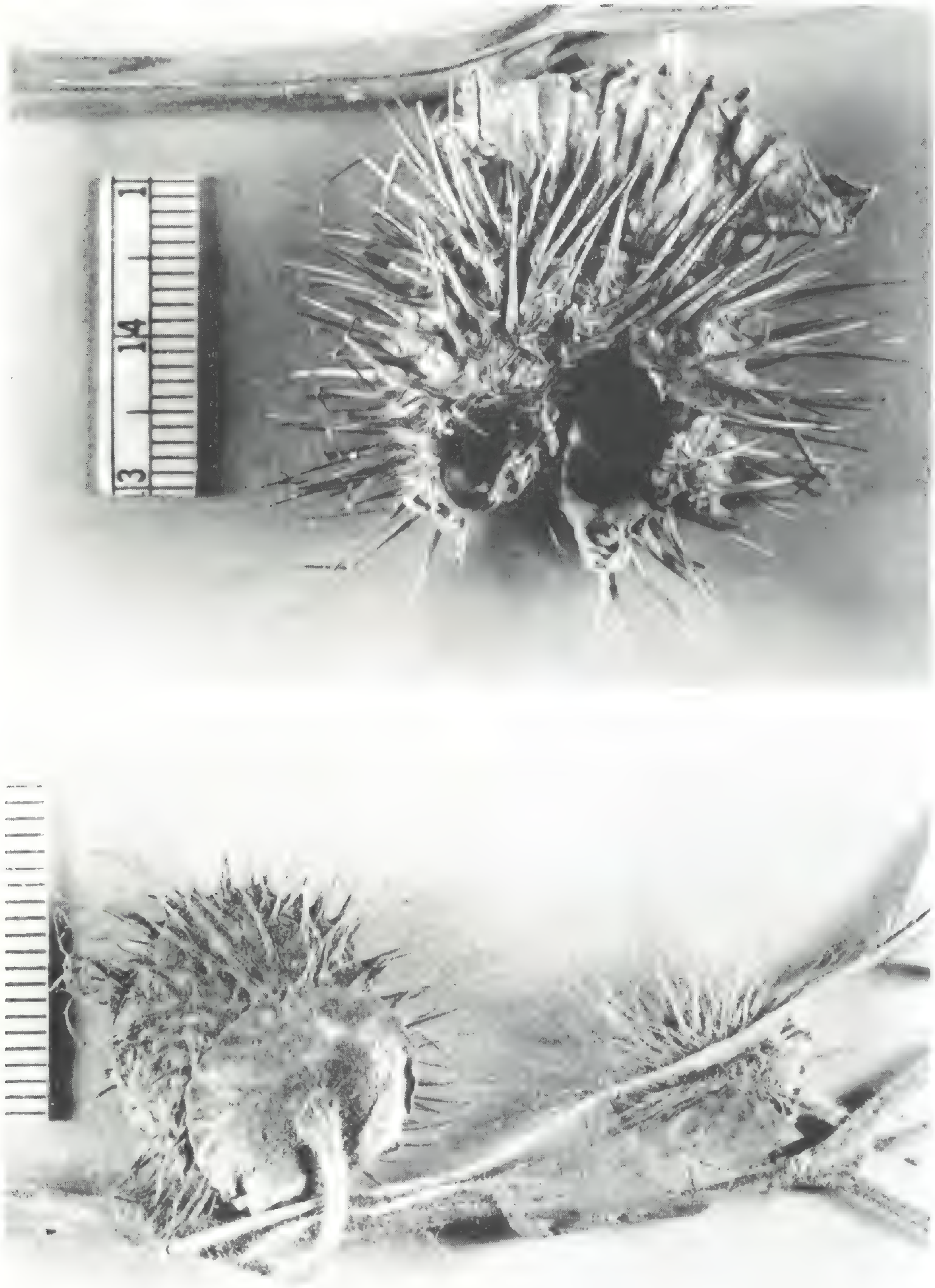
Perennial shrub or small tree reaching 3 meters or more in height; leaves alternate; blades up to 20 cm. long and up to 10 cm. broad, puberulent on both surfaces, ovate to ovate-elliptic in outline with an acute apex and a subequal base decurrent on the up-to-10 cm. long petiole; margins entire to irregularly sinuate-dentate; the larger, dentate leaves occurring on juvenile shoots with the smaller and entire ones on older branches; flowers axillary on somewhat arcuate, 1.5–2.7 cm. long pedicels; corolla tube basally green becoming light red which fades into yellow near the mouth, the veins red, interior of the tube deeply red tinged between the nerves, the upper half yellowish white, becoming deeply yellow near the mouth; calyx glabrous, somewhat inflated, cylindric, 4.5–8 cm. long, often split along one side giving a spathe-like appearance to it; calyx teeth two to four, unequal in length; corolla up to 20 cm. long, urceolate, terminating in a 5-dentate orifice, each tooth supported by three prominent nerves; the margin between the short and acuminate teeth slightly retuse; the five stamens free, epipetalous, extending to just below the mouth of the corolla, attached to the corolla tube at approximately the same level, 7–8.9 cm. from the base; filaments glabrous above, becoming villous near the point of adnation, anthers white, filaments pale green; shortly after anthesis the calyx dehisces at the base of the ovary and is shed; capsules obovate, deeply bisulcate with a secondary shallow division, up to 12 cm. or more in length, warty in appearance; seeds reniform, about 7 mm. long and 5 mm. wide, seed coat smooth on both sides, shiny, slightly

EXPLANATION OF THE ILLUSTRATION

PLATE LIII. *Upper:* Fruit of the type of DATURA REBURRA *Barclay* (*T. S. Brandegee*, s.n., Sept. 14, 1904). *Lower:* Fruit of the type of DATURA KYMATOCARPA *Barclay* (*G. B. Hinton*, No. 8173).

Photograph by CHARLES DILLS

Plate LIII



EXPLANATION OF THE ILLUSTRATION

PLATE LIV. *Upper:* Seeds of DATURA KYMATOCARPA *Barclay* (*Leavenworth*, No. 1615). *Lower:* Seeds of the type of DATURA REBURRA *Barclay* (*T. S. Brandegee*, s.n., Sept. 14, 1904).

Photograph by CHARLES DILLS

Plate LIV

EXPLANATION OF THE ILLUSTRATION

PLATE LV. DATURA VULCANICOLA *Barclay*. Photograph of the plant from which the type specimen was collected (*A. S. Barclay & R. E. Schultes No. 147*).

Photograph by RICHARD EVANS SCHULTES

Plate LV

EXPLANATION OF THE ILLUSTRATION

PLATE LVI. DATURA VULCANICOLA *Barclay*. Same as Plate LV in flower and fruit.

Photograph by RICHARD EVANS SCHULTES

Plate LVI

ridged on the convex side; chromosome number, 2n = 24.

COLOMBIA: Dept. of Cauca, Municipality of Puracé, northern slope of the Volcán de Puracé, alt. 2700–2800 m., July 23, 1956, *A. S. Barclay & R. E. Schultes 147* (TYPE: GH).—Same locality and date, *A. S. Barclay & R. E. Schultes 149 and 177* (GH).—Between Puracé and its páramo, Chiquín, heath-brush, alt. 2700–3100 m., July 11, 1939, *E. Pérez-Arbeláez & J. Cuatrecasas 5960* (F, US, COL.).—Puracé, alt. 3300 m., Feb. 1938, *K. von Sneidern 1898* (US).—Paletará to Calaguala, alt. 3000–3200 m., July 17, 1922, *F. W. Pennell 7093* (GH, NY, US).

In 1956, during my field studies of the tree Daturas in the Colombian Andes, I was surprised to find on the side of the famous and active Volcán de Puracé populations of what was at once distinguishable as a striking and beautiful new species of the genus. Herbarium specimens, fixed buds for cytological study, about 50 pounds of leaves for chemical analysis and living material in the form of cuttings and seeds for horticulture were gathered.

Earlier specimens which had been collected in the same general vicinity on the slopes of the volcano and which also represent the new species had been filed in our herbaria under the name *Datura sanguinea* Ruíz & Pavón. *D. vulcanicola* seems to be most closely related to *D. sanguinea* on the basis of comparative morphology.

Although *Datura sanguinea* is a highly variable species, *D. vulcanicola* may readily be distinguished from it by a number of characters, among the most prominent of which are its warty fruit and its smooth seeds. The fruit has a hard, almost woody pericarp and is attached to the branch by a stout peduncle which becomes nearly as thick as the branch supporting it. *D. sanguinea*, on the other hand, is characterized by its smooth, more fleshy fruit which is attached by an elongated, relatively unthickened peduncle and by its verruculose seeds.

The flowers of the new species are cernuous or nodding at a 30 to 45 degree angle, with a glabrous, nearly satin-

textured calyx and corolla. The light red to salmon-colored corolla tube fades into yellow near the mouth. The nerves are red, and the slightly inflated calyx tube dehisces after anthesis. In comparison, the flowers of *Datura sanguinea* are vertically pendulous, variously pubescent, and although the coloration is quite variable, the corolla tube is usually yellow becoming red towards the mouth with conspicuous greenish to yellow nerves. A much inflated calyx tube which is often persistent following anthesis forms a husk around the fruit.

Datura vulcanicola, as far as I could judge, does not reach the great height or corpulence which is commonly found in *D. sanguinea*. The chromosome number of 2n =24 (*A. S. Barclay & R. E. Schultes no. 147*) agrees with that of the other arborescent Daturas investigated.

In a communication to me, Professor Schermerhorn of the Massachusetts College of Pharmacy has related that a preliminary biochemical analysis of the leaves of this new species has shown no significant differences between the alkaloids present in *Datura vulcanicola* and in the other species of *Datura*.

Although *Datura vulcanicola* occurs in large numbers in the subpáramo heath vegetation under conditions which could be interpreted as wild, I am of the opinion that the abundance of individuals at the type locality is probably the result of human activity. My principle reason for believing this is that most of the plants were growing along what are or obviously had been foot paths or donkey trails. Furthermore, we must not overlook the fact that for centuries this agriculturally rich volcanic area has been populated by advanced Indian peoples who are known to have employed Daturas as narcotics in their magic and therapeutic practices. It is interesting to note in this connection, however, that *D. vulcanicola* has not been spread, at least to any appreciable extent, from this

locality by primitive man. It may yet be found on neighboring mountains, but neither the comparatively thorough explorations in this general area in the past nor my own collecting, directed almost exclusively to *Datura*, have turned it up elsewhere.

Acknowledgments

I would like to acknowledge the help and encouragement of my major professor, Dr. R. C. Rollins, who made available to me the Fernald Fund of Harvard University for field work in South America. I also owe a debt of gratitude to Dr. R. E. Schultes who first suggested the genus *Datura* as a research subject and whom I had the privilege of accompanying while in South America. To Dr. Jesús M. Idrobo, Dr. Alvaro Fernandez-Pérez and the other members of the Instituto de Ciencias Naturales, Bogotá, Colombia, I wish to extend my deepest gratitude and appreciation for their kindness and help during my stay in their country.

BIBLIOGRAPHY

Dandy, J. E. 1958. The Sloane Herbarium. British Museum, London. 166.

Dunal, F. 1852. Solanaceae [*Datura*] in Alphonse de Candolle Prodromus, 13, pt. 1: 538–546.

Ewan, J. 1944. Taxonomic history of the perennial southwestern *Datura meteloides*. Rhodora 46: 317–323.

Gray, A. 1878. Synoptical Flora of North America, 2, pt. 1: 240.

Leavenworth, W. C. 1946. A preliminary study of the vegetation of the region between Cerro Tancitaro and the Rio Tepalcatepec, Michoacan, Mexico. American Midland Naturalist. 36: 137–206.

Leopold, A. Starker. 1950. Vegetation zones of Mexico. Ecology. 31: 507–518.

Miller, P. 1768. The Gardener's Dictionary, ed. 8. (*Datura* n. 5).

Regel, E. von. 1859. *Datura Wrightii* Hort. Gartenflora 8: 193, t. 260.

Safford, W. E. 1921. Synopsis of the genus *Datura*. Jour. Wash. Acad. Sci. 11: 173–189.

Timmerman, H. 1927. *Datura:* the nomenclature of the species used in medicine. Pharm. Jour. (London) 118: 571–574.

THE PRESENT DISTRIBUTION OF NARCOTICS AND STIMULANTS AMONGST THE INDIAN TRIBES OF COLOMBIA

BY

NESTOR USCATEGUI M.[1]

RECENT extensive and intensive interest in narcotic and stimulant plants on the part of medical and pharmacological investigators has focused attention on the need of knowing more about these plants from the botanical and anthropological points of view. During the past twenty years or so, significant strides have been made in determining the correct botanical sources of plant narcotics and stimulants. Very little has been done, however, toward bringing into some semblance of order the vast amount of information on their distribution, preparation, use and social significance, which is scattered here and there throughout ethnological literature and the writings of travellers.

Forasmuch as Colombia represents one of the regions of the world where the native population has developed to its highest degree the use of plants which act on the central nervous system as intoxicants or stimulants, I propose here to present a preliminary and very much abbreviated survey of the distribution of the use of these plants amongst the Indians of this country.

[1] Instituto Colombiano de Antropología, Bogotá, Colombia.

I.

The population of Colombia is a racial mixture that is constantly increasing in complexity. It consists in great part of Europeans, especially from Spain, and of Indians from Middle America, the Antilles, the northern Andes and the Amazonian regions. There are also some negroes, mostly from Africa, who have intermingled with both whites and Indians, especially in some of the Departments. All these groups have contributed their share to the spiritual and cultural complex which man represents in Colombia.

Much of Colombia, sparsely populated and with a dearth of roads, is occupied by Indian tribes which subsist wholly on local resources. The rivers provide these natives with roads, meat and drink; the plant kingdom furnishes their clothing, shelter, food, medicines, stimulants, narcotics and poisons; the animal world supplies food, diversion and other material for magic.

These Indians employ sundry stimulants and narcotics of great potency in both magico-religious rites and in daily life as well. The accompanying map shows the wide distribution of the use of such plants. This is so great that it causes us to wonder why such a complex exists in Colombia.

Many of the naturalists, ethnographers, explorers and geographers who have lived or travelled amongst these Indians have attempted to interpret the reason for the extensive use, and even near-abuse, of stimulants and narcotics in this area. Actually the reason is simple: it is due merely to primitive mentality which is mystical. The Indian considers all nature and the visible and imagined cosmos to be endowed with spirit-forces. He does not recognize any boundary between natural and supernatural phenomena. This reason is in concord with that of Pardal (27) and Frazer (14), but is not in agreement

Plate LVII

Distribución de las Tribus Indigenas de Colombia que emplean Narcóticos y Estimulantes
Atlantico
Oceano
Pacifico
Panama
Venezuela
Ecuador
Peru
Brasil
GUAJIRO
GUAJIRA
IKA
KOGI
SANKA
MAGDALENA
CHIMILA
MOTILON
BOLIVAR
CORDOBA
NORTE DE SANTANDER
SANTANDER
ANTIOQUIA
CHOCO
CHAMI
CALDAS
TOLIMA
VALLE
CAUCA
HUILA
PAEZ
GUAMBIANO
NARIÑO
SIBUNDOY
PUTUMAYO
CORREGUAJE
CAQUETA
ANDOKES
SIONA
KOFAN
CUNDINAMARCA
Bogotá
BOYACA
CASANARE
ARAUCA
TUNEBO
SALIVA
PIJAO
PIAPOKO
GUAHIBO
SIKUANI
META
ARAWAK
GUAYABERO
PUINAVE
VAUPES
KURIPAKOS
SIUSI
KARIHONA
DESANO
TARIANO
GWANANO
KUBEO
TAWAINOS
MAKU
TUCANO
TUYUKA
BARASANA
MAKUNA
TAMINUKA
MUINANE
MIRANA
YUKUNA
WITOTO
ROSSIGARO
BORA
OKAINA
AMAZONAS
TIKUNA
Rio Meta
Rio Guaviare
Rio Inirida
Rio Vaupes
Rio Caquetá
Rio Putumayo
Rio Negro
FAMILIA LINGUISTICA
ARAWAK
CHIBCHA
GUAHIBO
KARIB
TUCANO
KECHUA
WITOTO
NO CLASIFICADO
KOCHE

with Taylor's animism theory (48) or Levy Bruhl's prelogical mentality hypothesis (23). There are other more recent theories which, because of the brevity of this article, I do not mention, and which likewise fail to accept a simple explanation for the use of narcotics. Unfortunately, some anthropologists, in studying native peoples, like to presuppose a complex type of mentality. In doing so, they accomplish nothing; on the contrary, they tend only to complicate what is obvious, logical and simple.

Insofar as the narcotics and stimulants are concerned, it has been shown that the highest cultures of America used these plants for religious or magical purposes and that, when the Spanish conquest broke down their religious, social and economic structure, these uses passed from the priestly and noble classes down to the masses who seized upon them to help solve their post-conquest problems. If the employment of narcotics sometimes developed into a commercial exploitation—as with coca in Peru and Bolivia—the immediate cause of this evil lies in intervention by white men (50). The native never looked upon his narcotics and stimulants as sources of pecuniary advantage. In pre-Columbian times, amongst American cultures of lower material and spiritual development, narcotics and stimulants were also used; and they continue to be used at the present time. Likewise, there has always existed—and there still exists—a magical or religious motive for their employment (52).

This is the field in which my own interest lies: an historical and social study of the native cultures of Colombia which are characterized at present by the widespread use of these plants. I am referring here only to present-day cultures, for to discuss the pre-Hispanic civilizations would demand too extensive a treatment.

In an earlier article (50), I have considered the chemical and therapeutic studies which have been made on coca.

These obviously have great practical importance, and the world-wide utilization of the active principle is outstandingly beneficial to man. Nevertheless, I must point out that the chemical studies of these narcotics and stimulants are far from complete. This is due primarily to the poor quality of properly identified materials on which previous investigations have been based. Furthermore, medical and therapeutic studies have usually been made on animals and in surroundings completely different from the natural environment.

The experiences realized personally by some of the naturalists and ethnographers in the use of these plants, so to speak *in situ*, have relative value, and, together with detailed descriptions by travellers or trustworthy natives, they give us some idea of the actual effect of these plants on man. Without in any way detracting from these investigators, we must say that in their accounts of the uses, kinds, collection, preparation, ceremony, symbolism and mythology of narcotic and stimulant plants most writers offer very incomplete data and usually fail to preserve material on which definite botanical determinations may be made. Furthermore, in the case of those naturalists of the past century who wrote down careful notes on the uses of plants and gathered specimens which permitted proper identification, the name of the tribe involved was often not critically determined.

My own experiences with some of the tribes of Colombia, my personal contacts with other investigators with field experience and my recent study of the literature have made it possible for me to clarify and amplify many points which hitherto have been poorly understood. My former purely ethnological approach has, during the past year, been enriched by a botanical panorama, especially in the field of narcotics and stimulants, made pos-

sible by the use of the extensive and extraordinarily well organized libraries and museums at Harvard University and by my associations with botanists at this institution.

The present very brief paper on the overall distribution of the use of narcotics and stimulants in Colombia is offered merely as an introduction to a longer and more detailed work on the subject which I am preparing as a Guggenheim Fellow in Ethnobotany at the Botanical Museum of Harvard University.

For help and advice on numerous points, as well as for editorial assistance, my thanks are due especially to Dr. Albert F. Hill and Dr. Richard Evans Schultes of the Botanical Museum of Harvard University; and to Miss Siri von Reis and Mr. Arthur S. Barclay of the Gray Herbarium of the same University. I also wish to thank Miss Ruth Barton for her skillful execution of the map.

II.

Principal narcotics and stimulants used by native tribes in Colombia

Common name	*Identification*	*Distribution*
Coca	*Erythroxylon Coca* Lamarck	Peru, Bolivia, Ecuador, Colombia
	Erythroxylon novogranatense (Morris) Hieronymus	West Indies, Trinidad, Peru, British Guiana, Venezuela, Colombia (15)
Yajé	*Banisteriopsis Caapi* (Spruce ex Grisebach) Morton	Colombia, Brazil, Bolivia, Peru
	Banisteriopsis inebrians Morton	Colombia, Ecuador, Peru
	Banisteriopsis Rusbyana (Niedenzu) Morton	Colombia
	Tetrapterys methystica R. E. Schultes	Brazil (and Colombia?)
Yopo	*Piptadenia peregrina* Bentham	Antilles, Guianas, Venezuela, Colombia, Brazil
Yakee, Yato, Paricá	*Virola calophylla* Warburg *Virola calophylloidea* Markgraf	Colombia, Brazil, Peru, Venezuela

Mets-kwai borrachera	*Methysticodendron Amesianum* R. E. Schultes	Colombia
Tonga, Borrachera	*Datura suaveolens* Humboldt & Bonpland ex Willdenow	Colombia, Ecuador, Peru
	Datura candida (Pers.) Safford	
	Datura arborea Linnaeus	
	Datura sanguinea Ruíz & Pavón	
	Datura dolichocarpa (Lagerheim) Safford	
Tobacco	*Nicotiana Tabacum* Linnaeus	Widespread (16)
Yoco	*Paullinia Yoco* R. E. Schultes & Killip	Colombia, Ecuador, Peru

III.

Distribution according to linguistic groups

In view of the lack of any adequate cultural classification of the Indian tribes in Colombia, I am considering the various groups in accord with a linguistic classification, realizing, at the same time, that this has really very little significance insofar as the use of narcotics and stimulants is concerned. I am also discussing the tribes in order from north to south along the Andes and Pacific coastal regions and then across the Amazon valley to the llanos or Orinoco basin.

Guajiro: linguistic family *Arawak*, according to Rivet (38).

The Guajiros inhabit the desert area of the Guajira Peninsula in northeastern Colombia. They employ a tobacco-paste which they chew, especially for magical purposes. The *piache* (witch-doctor) uses a piece of *manilla*, tobacco-paste brought in from Rioacha in the Departamento del Magdalena, Colombia, or from Maracaibo in Venezuela. If *manilla* be unavailable, leaves of *macuira*, a plant similar to tobacco, are chewed to bring about a state of trance for divination (28).

At the present time, the cigars and cigarettes of the

white man have become favorites and must likewise be imported, since the climate of the Guajira makes the cultivation of good tobacco impossible. In spite of the restrictions imposed by the climate, I believe that the use of tobacco is an old culture-trait, associated (in the period of the Conquest and in Colonial times) with the employment of coca or *hayo* for chewing, a habit borrowed probably from the neighboring Indians of the Sierra Nevada de Santa Marta. This is attested to by several chroniclers (10, 19). It seems also to be supported by its marked connection with magic; for the *piache* (man or woman), believes himself to be appointed by Wanurú, Spirit of Death, and begins his intoxication by chewing tobacco for several days until a state of ecstasy is attained (29). This ecstasy brings to mind that of the Kogi priests from the Sierra Nevada who induce similar semi-narcotic states through taking coca mixed with concentrated tobacco-water. Differences in concentration of this tobacco-extract account for the different names: *noai* and *mo* or *chimó* (12) referring to a thick paste or jelly-like extract, *ambire* or *ambirá* to the liquid extract or water. It seems that this culture-trait passed from the Sierra Nevada de Santa Marta to the Venezuelan Andes and thence to the east-central region of that country. The Guajiros acquired it at the same time they acquired coca-chewing. Due to difficulty in transporting coca, which cannot be grown in the Guajira, coca-chewing died out, the custom surviving only in magic rituals with the chewing of tobacco or *macuira*-leaves, instead of coca (50, 51).

Kogi, Ika, Sanka: linguistic family *Chibcha*, according to Rivet (38), Holmer (17).

These tribes are known under the generic name Arauacos or Arhuacos, an epithet causing considerable confusion with the name of the linguistic family Arawak.

They dwell on the eastern slopes of the Sierra Nevada de Santa Marta in the northern part of the Departamento del Magdalena (36).

The ancient culture-trait of coca-chewing is conserved amongst these Indians. The coca or *hayo* is mixed with tobacco-extract, *ambirá* (53). Proof of the antiquity of the custom is given by references to it in the chronicles of the Conquest and Colonial periods. Archaeological evidence, especially such finds as stone masks depicting coca-chewing — masks analogous to wooden ones made by these people today — relates these tribes and this culture-trait to the Taironas or Tairos. Linguistically, the word *hayo* stems from Tairona. Furthermore, there are certain other vestiges which indicate that the cultures of the Sierra Nevada have continued for over five hundred years some of the older and similar Tairona culture-traits (50).

Coca and tobacco, amongst the Sierra Nevada Indians, play a wholly religious role and are used in order 1) to enable the subject to fast, 2) to attain complete sexual abstinence, 3) to keep from sleeping and 4) to refrain entirely from speaking of the "ancestors" (that is, to avoid dancing and reciting) (37).

Only the males employ tobacco and coca, because of a strong religious taboo which is widespread throughout Andean cultures.

Coca-plots are put in beside every house or around settlements, where they occupy as much land as is possible, as well as in distant fields. These Indians distinguish three kinds of coca, each kind belonging to different tribes. One variety with long leaves (grown by the extinct Kamkuama tribe); one with small leaves (Kogi); and one with very minute leaves (Ika). Furthermore, it is said that "the ancients" used a tree (unfortunately not determined botanically) of the high moors or *páramos*

with leaves like coca and called *guanguara* or *guanguala*.

Any person desiring to plant coca must get leaves from the *máma* (priest). Cultivating and working the land is man's work; but harvesting the leaves is woman's task. As coca is a perennial, the leaves can be gathered at any time of the year, The men prepare coca in the houses, a very painstaking chore, since coca is a sacred tree and must be duly respected when it is handled. The leaves are first cleaned of insects, petioles and damaged parts, and are then dried. Then they are put into a pot kept only for this purpose and are toasted over a slow fire in the ceremonial hut. Constant stirring is necessary, for they must not be dried too much, in order to retain a bright green color. When ready, the leaves are put into a small cotton bag (36).

As elsewhere, coca leaves must be mixed with lime before chewing. This alkaline agent is made by burning the shells of bivalves found on the Atlantic Coast. The burning is done on a small pyramidal pile of grasses, and the lime is gathered up in a bottle-shaped gourd (*Cucurbita Pepo*). The gourd, once filled, becomes for its owner a life-long companion; for in the initiation rites, young men are given the gourd and told that it symbolizes woman. The young man is married to this "woman" during the ceremony, and he perforates the gourd in imitation of defloration.

The introduction into the gourd and the rubbing motion of the stick are interpreted as coitus, and, culturally, it is understood that all true sexual activity should be repressed and should be expressed only in the use of coca. All biological needs, all frustrations, are thus concentrated in this tiny instrument which, to the Indian, represents *food*, *woman* and *memory* (36).

Tobacco, amongst these people, is taken according to the native, to make coca more agreeable. Tobacco plots

are located near the houses, and their cultivation is left to the men. Women gather the leaves.

As in the case of coca, tobacco has a part in the mysticism of these Indians. Tobacco-concentrate, *ambira*, which, like coca, is kept in a gourd, is prepared by a long steeping of the leaves and by mixing the resulting liquid with *yuca*-starch (*Manihot utilissima*) and *sugii* (*Sorghum* sp.). There is a certain similarity between the use of tobacco in this form and that characteristic of the Witotos of the Amazonas, and, in fact, there is some analogy in the mythology of these two groups of Indians (50).

Motilon: linguistic family *Karib*, according to Rivet (38).

The Yuco, as they call themselves, who live in the Sierra de Perijá, Departamento del Magdalena, belong to the Karib group, but the famous "Motilones" of the Catatumbo appear to be Arawaks (32).

This tribe grows tobacco in a rather primitive manner. In preparing tobacco, they merely hang leaves from the rafters of the houses to dry. The dried tobacco is carefully kept in baskets by the men. Smoking is done only in pipes. Both sexes and all ages smoke, children passing from their mother's breast to pipes. The pipes are of clay with a wooden stem (33).

It seems that the Yuco knew of coca and chewed it until very recently. It has now completely disappeared. Yuco coca-chewing was probably due to commercial relations with the Indians of the Sierra Nevada, for the Yuco did not grow coca, notwithstanding an appropriate climate, and, significantly, it was that fringe of the Motilones nearest Sierra Nevada which knew of the coca-chewing custom.

Chimila: linguistic family *Arawak*, according to Reichel-Dolmatoff (31).

A primitive Indian group, the Chimilas live in the extensive forests occupying the basins of the Magdalena, Ariguaní and Cesár Rivers.

Tobacco-chewing is practiced by the oldest inhabitants. Dried leaves are pulverized between two stones and to the powder is added a small quantity of ashes and some honey. Small cakes about two centimeters long are made of this mass. Occasionally, one may see thick cigars of Chimila-grown tobacco, but the usual way in which the male members of the tribe employ the narcotic is in chewing.

Chami: linguistic family *Karib*, according to Rivet (38).

The Chamí live in Corozal, Municipio de Río Frío, Departamento del Valle.

These Indians have a tobacco-pipe in the form of a small vase with four appendages on the basal edge by means of which four persons at a time smoke the narcotic. This ceramic is exceptional: a collective pipe of such singular construction represents a culture-trait hitherto unsuspected and can logically be considered a ceremonial object. The discovery of clay elbow-pipes also gives us reason to suspect that smoking amongst the Chamí was ceremonial (34, 11).

Pijao: linguistic family *Karib*, according to Rivet (38).

The Pijao comprise three groups representing one ethnic unit living in the southern part of the Departamento del Tolima.

Coca is found amongst these Indians and is used by them in the same way as by the neighboring Paez. Since coca is infrequent amongst Karib tribes and since the Pijao have been neighbors of the Paez from the time of

the Conquest, the trait was probably borrowed by the Pijao from their Chibcha neighbors, the Paez, just as the Motilones borrowed it from the Chibchan groups of the Sierra Nevada, and Karib groups in the Amazon acquired it through contact with other tribes (35).

Choco: linguistic family *Karib*, according to Rivet (38a).

These Indians live in scattered groups along the Pacific coast and in the headwaters of the Río Condoto in the Departamento del Chocó.

Some groups of the Chocós use *Datura* (possibly *D. suaveolens*) in magic. According to Wassen (54), these natives probably employ a species of *Datura*, and Seemann (41) asserted as early as 1852 that the Indians of the Chocó prepare a decoction of *Datura* seeds which is sometimes given to children in maize-beer, in which drink its ill effects are said to be counteracted. The Indians believe that persons under the influence of *Datura* (*tonga* or *borrachera*) have the power of divination.

Paez: linguistic family *Chibcha*, according to Rivet (38), Ortíz (26).

This is the largest tribe in Colombia, numbering about 30,000. It is distributed as follows: one part in the Departamento del Tolima, between the Atá and Saldaña Rivers; another and major part in the region called Tierradentro in the northeastern section of the Departamento del Cauca.

The Paez have grown and used coca for more than four centuries. Coca cultivation is carried on in the valleys crossed by the Paez River and up to 2000 meters in altitude.

Amongst these people, coca is mainly a dietary complement, but it is also used in magic and medicine. All

members of the tribe, without regard to sex or age, chew coca, and they traffic in it, using it as a monetary medium (50).

As in all Chibchan groups, men plant coca and women harvest it. This is partly in accord with division of work between the sexes and partly in accord with tradition. I believe that, insofar as the women are concerned, there is a magico-religious taboo; but this has in part disappeared due to the influence of Catholic missions and consequent acculturation, even though coca is used in magic in all twenty Paez reservations and the usual Indian mentality is still dominant throughout the Paez population.

Coca leaves are toasted over a slow fire in great earthen pots. When the leaves are dark green with a golden or straw-colored sheen, they are ready for use. They are carried in woven woollen bags, which every Paez Indian wears hanging from the neck. The lime is provided from limestone, abundant in the region, which is broken up by fire. It is kept in a small gourd carried in the coca-bag.

The "chewer" takes a few dried leaves from the bag and places them in the mouth where they are moistened and rolled into a pellet with the tongue. Then a small amount of lime is extracted from the gourd with the fingers, placed in the mouth and mixed with the chewed leaves. This produces the desired effects.

The Paez likewise chew tobacco, principally in magic and medicine (1). Generally, they do not cultivate the plant, buying manufactured cigarettes for the purpose. The shaman employs tobacco mixed with coca during magic-sessions. It seems that the intrusion of tobacco into Paez medicine is not very old. *Borrachero* (a species of *Datura*) is used by the witch-doctor as a venomous narcotic to cause enemies to become insane (1).

Guambiano: linguistic family *Chibcha*, according to Rivet (38).

The seven thousand Guambianos, who dwell in the western part of the Departamento del Cauca, use coca magically in those reservations economically most advanced (Quizgó and Guambía) and in Ambaló as a dietary supplement, but naturally with magical connotations. Coca cultivation has decreased appreciably. The preparation of the leaves is the same as amongst the Paez (50).

Sibundoy: linguistic group *Koche*, according to Ortíz (26b).

The Sibundoy Indians, speaking Kamsá, live in the eastern half of the Valley of Sibundoy.

In their magico-therapeutic rites, they make use of a number of solanaceous plants: *Datura candida*, *D. sanguinea* and *D. dolichocarpa*. Each of these species of *Datura* has its special native name. There are further, according to Barclay and to Schultes, bizarre forms of these species with deformities due probably to virus-infection, each of which the Indians recognize as a different "kind" of *borrachero* and each destined for a specific magico-therapeutic use. The Sibundoy also possess another curious solanaceous drug, an endemic of their high, mountain-girt valley: *Methysticodendron Amesianum*.

The use of these highly dangerous solanaceous narcotics is restricted to the medicine-men who employ them for divination, prophecy and therapy. The intoxicating effects, which may reach the point of delirium, sometimes last up to several days, with periods of utter unconsciousness.

Only the leaves are used in preparing the intoxicating drink, the infusion taking from thirty minutes to one hour to prepare. The medicine-men never imbibe the liquid all at once, delaying the drinking ceremonially over a two or three hour period. In the case of *Methy-*

sticodendron, tradition dictates that the drug must be taken during the wane of the moon. *Yajé*, coca and tobacco are doubtlessly present as imported curiosities in the bundles of magic-elements of Sibundoy medicine-men, but none of these narcotics is used widely by the Kamsá people (46).

Siona: linguistic family *Tukano*, according to Rivet (38), Loukotka (24), Castellví (3), Ortíz (26).

Inhabitants of the Comisaría del Putumayo, between the Sucumbíos and Guamüés Rivers, these Indians are allied linguistically and culturally to the Tukanoan tribes of the Vaupés, from which region they probably came, perhaps at an earlier date than the only other western Tukanoan group, the Koregwahes. They have lived in their present locality, however, at least since Colonial times and have probably adopted some of the narcotics and stimulants from their non-Tukanoan neighbors.

The Sionas use tobacco in the form of cigars and concentrated extract (2). They prepare tobacco in a most curious way which is, in reality, a combination of the cigar-making of the Vaupés Tukanos and the *ambíl*-making of the Witotos: they add peels of unripened bananas and cacao husks, burned and sifted, to the extract. Furthermore, they smoke cigars and use the long, communal ceremonial cigar of the Tukanos of the Vaupés. But they do not, as do the Tukanos and Witotos, use coca, the place of which is filled by *yoco*.

Yoco, a stimulant rich in caffeine, is one of the principal economic plants of the Sionas. Schultes believes that the origin of the use of *yoco* may be Kechwa, since its name, used by all the Indians of the Putumayo regardless of their linguistic affinities, is apparently derived from Inga, a splinter tribe, once numerous, located in the region of Mocoa, speaking a dialect of Ecuadorean

highland Kechwa. There is, however, as Schultes points out, no real proof on which to base such a theory (45).

They also take *yajé*, making use of *Banisteriopsis quitense*, *B. inebrians* and *B. Rusbyana*. From these narcotic lianas, they prepare a drink employed preferentially by the witch-doctors for magic purposes. Occasionally, other plants are added to the *Banisteriopsis*, some of which are not malpighiaceous: a species of tree-*Datura*, the amaranthaceous *Alternanthera Lehmannii* and, sometimes, tobacco-leaves (47).

Kofan: linguistic family *Chibcha*, according to Rivet (38) and to Jijón y Caamaño (18a); family uncertain or unknown according to Ortíz (26) and to Mason (24a). Cf. Castellví classification (4).

The Kofáns are located near Puerto Ospina on the Putumayo River and on the Sucumbíos and Guamüés Rivers in the Colombian Comisaría del Putumayo and along the Aguarico River in adjacent Ecuador.

Tobacco is important to the Kofáns. It is used in long rolls or pressed cakes, similar to those found amongst the Tukanoan groups of the Vaupés. Both tribes now import the rolls from Brazil. The Kofáns use also the concentrated extract, which they call *ambíl*, as do the Witotos of the Amazonas (51).

Yajé, made especially of *Banisteriopsis inebrians* and probably also of *B. quitense*, is one of their more important narcotics, and its use is not confined to the priestly or doctoring class.

The Kofáns are the most excessive users of *yoco*, which is consumed daily by all individnals. When the wild supply of this forest vine is exhausted in a region, an entire settlement may move in order to locate itself near a new and adequate supply. It is never cultivated, since it is such a slow-growing liana (47).

Inga: linguistic family *Kechwa*, according to Ortíz (26b).

This reduced group of Indians, now living near Mocoa in the Comisaría del Putumayo, is probably a remnant of a former Kechwa expansion from the highlands eastward over the slopes of the Andes in southern Colombia.

These Inga Indians are much given to the use of *yajé*, made normally of *Banisteriopsis inebrians* or *B. Rusbyana*, sometimes with non-malpighiaceous admixtures. They refer to the narcotic also as *ayahuasca*, a generalized Kechwa name meaning "vine of the dead." *Yajé* also finds use amongst the Ingas as a violent purgative. For magical purposes, *yajé* is taken sometimes only by the shaman and sometimes by any male member of the tribe under the supervision of the shaman (47).

The Ingas likewise use *yoco* daily as a stimulant. Coca is never chewed by members of this tribe (45).

Koregwahes: linguistic family *Tukano*, according to Rivet (38), Mason (24a).

The Koregwahes, like the Sionas, probably came westward from the Vaupés in pre-Colonial times, but apparently at a later date. Quite possibly they brought the coca habit with them.

Unlike the Sionas, however, they do not use tobacco, but have adopted *yoco* and *yajé*. I cannot dare to guess from whom they borrowed the use of *yajé* (8), because almost all of the tribes of the Putumayo, Amazonas and Vaupés use it.

Witoto: linguistic family *Witoto*, according to Koch-Grünberg (20), Rivet (38), Castellví (7), Ortíz (26).

The Witotos are dispersed in several localities of the Colombian Comisaría del Amazonas, especially along the Karaparaná and Igaparaná Rivers, and in adjacent parts

of Peru. The tribe suffered dismemberment through the exodus of many groups around the first of this century, as a result of persecution during the rubber boom. Due to years of harsh treatment as virtual slaves in rubber work, they suffered also much cultural disintegration in this period.

They use a tobacco-concentrate, a syrup-like or semi-solid extract of a deep brown color, called *yera*, *yeras* or *djerabe* (49, 21, 6).

The largest and greenest leaves from the lower part of the plant are boiled slowly in a large earthen pot for several hours. Before the extract becomes thick, it is taken from the pot, and alkaline salts are added to it. These salts are prepared from the petioles and leaves of a species of *Chamaedorea* and from the young shoots of a species of *Bactris*. They are called *cha-pe-nas* in Witoto and are obtained by the evaporation of the water which has been passed through the ashes of the aforementioned plant materials (42).

The preparation of *ambil* differs little amongst the sundry groups of Witotos, and this culture-trait has its roots deep in Witoto history and mythology (28). There is a surprising similarity between this use of tobacco, and that of the tribes of the Sierra Nevada de Santa Marta. To explain this through cultural parallelism would be too premature, and it is necessary to delve a bit deeper into the history and mythology of the two tribes to arrive at a satisfactory solution.

Usually the Indians employ *ambil* together with coca, but they occasionally use it alone. Witoto women do not chew coca, though some take tobacco. It would seem that the vestiges of an ancient taboo against the use of these narcotics by women still exists (50).

Coca preparation likewise presents reminders of ancient ceremonials. The fresh green leaves, toasted brown in an

earthen pot, are pulverized, and the powder is mixed with ashes of the *yarumo* trees (*Cecropia* spp., especially *C. peltata* L.). This mixture is sifted through pounded bark-cloth and is thus made ready for chewing (42).

Even though the use of these two plants has lost much of its ancient ritualistic savor, they are still taken at important or special meetings or councils, where critical tribal business is discussed or tribal history and tradition are recited (25).

One naturally finds certain slight variations in the preparation of tobacco and coca within the Witoto groups, especially between the Witotos themselves and the Boras. The Boras live more apart from missionary influence than do the Witotos to-day and, consequently, have preserved more of their old traditions and indigenous culture. Some students, such as Rivet (38), believe that the Boras belong to the Tupí-Guaraní linguistic family, whereas others, like Castellví, hold them to represent a distinct family. Jijón y Caamaño (18a) maintains that the Boras are related to the Witotos. My personal belief is that only a closer study of the Bora language can solve this riddle, even though it is clear from the reports of reliable travellers that Witotos and Boras converse together in their respective languages and understand one another with difficulty. Culturally, however, the Witotos and Boras, neighbors for centuries, are extremely close, and we have discussed them here with the Witotos for this reason.

Cigars are smoked amongst some of the Witoto groups to the north. The cigar is made with a banana-leaf wrapping and the tobacco is that commonly cultivated by the Witotos (51, 18).

Finally, we can point to the use by the Witotos of the hallucinogenic narcotic *ayahuasca* or *yajé* (*Banisteriopsis* spp.), though apparently on a rather reduced scale. Here

the use of *ayahuasca* is commonly restricted to the shaman and has not extended itself to the whole population.

The Miraña (Miranya) Indians, now much reduced in numbers but once widely feared for their war-like characteristics, are usually classified linguistically as Witotoan. According to information which I have received from travellers and others who know the Mirañas, I believe that there may be very good reason for suspecting that they are not Witotoan and that they may perhaps constitute even a distinct family. They now dwell near La Pedrera on the Caquetá River and along the lower reaches of the Kawinarí River, a southern tributary of the Caquetá. There are also groups of Mirañas in adjacent Brazil.

Because of long proximity, the Mirañas are culturally, in many respects, similar to the Witotos and Boras. They use coca in large quantities in daily life and are said to employ tobacco in the form of snuff and *ambíl*. There seems to be no report that they take *caapi*.

Tukano: linguistic family *Tukano*, according to Rivet (38), Castellví (5), Mason (24a) and others. Cf. the classification of Koch-Grünberg (21).

Tukano represents one of the most important linguistic families of South America. The sundry Tukanoan tribes dwell for the most part in the Comisaría del Vaupés and in adjacent Brazil. The more important tribes in the Colombian Vaupés are the Gwananos, Piratapuyos, Taiwanos, Makunas, Barasanas and Djis. The Kubeos are usually classified as Tukanoan, but there may be reason for questioning their belonging to this linguistic family. They represent the culture of the tropical forest, are agriculturists, fishers, river-travellers, use the hammock and know the art of ceramics. Socially, they are fratricidally organized (14a).

Tobacco, coca, *pariá* and *caapi* are the narcotic plants that figure in their daily life as well as in therapeutic and magic rites (43, 47, 50, 51).

The great cigar, made from rolled tobacco leaves covered with leaves of maize, banana or other plants or with the soft inner bark of an unidentified annonaceous tree, is characteristic of the Tukanos. Held in an artistically turned forked wooden support, this three-foot cigar is smoked in certain festival ceremonies. Its use is, however, on the wane (51).

Tobacco is also the basis of a snuff amongst these Indians. The leaves are dried and pulverized, and the resulting brown powder is mixed with an equal amount of ashes from any of a number of plants. The final snuff is greyish. Both sexes may partake of tobacco-snuff which is rather commonly used. It is kept in a case made from large land-snails with a tube or mouth fashioned from a bird bone.

Banisteriopsis is taken by any male member, even though its use is essentially in magic. It is customarily employed during various dances which take place more frequently during the rainy season. Occasionally, treatment of disease or exorcism are practiced during *caapi*-dances. *Caapi* is perhaps best known as the strong narcotic given to enhance the bravery of Tukano boys about to undergo the violent physical ordeal connected with their initiation ceremony—the Yurupari Dance (47).

The Tukanos likewise use a snuff prepared from the blood-red resin of certain species of the myristicaceous tree, *Virola*, especially *V. calophylla* and *V. calophylloidea*. It is commonly known as *pa-ree-ka* amongst the Tukanos, though this is a Tupí-Guaraní loan-word. The Puinaves call this intoxicating snuff *ya-kee*, the Kuripakos *ya-to*. It is prepared by boiling the resin for many hours and allowing it to sun-dry to a hard mass which is

then pulverized. An alkaline admixture of ashes of bark from a species of wild cacao-tree (*Theobroma subincanum*) is added to the powder, and the resulting preparation is sifted to form the final snuff. Unfortunately, this has been widely confused in anthropological literature with an intoxicating snuff made from the leguminous seeds of *Piptadenia peregrina*, a narcotic used in Colombia by non-Tukanoan tribes inhabiting principally certain western tributaries of the Orinoco River (43, 43a).

Desano and **Tariano:** linguistic family *Arawak*, according to Rondon (39a), and Schultes (personal communication). Cf. the classification of Koch-Grünberg (22).

These two Arawak tribes live along the lower part of the Colombian course of the Vaupés River and on affluents of it, in a long and close geographic and cultural proximity to the Tukanoan groups of the region.

Their use of coca, *caapi* and tobacco are similar in all respects to those of the Tukanos. They also know and employ *paricá* or *Virola*-snuff as do their Tukanoan neighbors (43).

Tikuna: linguistic family *Arawak*, according to Castellví (3).

The Tikunas live in the Trapecio Amazónico of Colombia and adjacent parts of Brazil and Peru. They employ tobacco in the form of a cigar (9, 25a), and there are reports that they conserve the use of the pipe for smoking (51, 25a). They likewise use *paricá* or *Virola*-snuff. I once believed, on the basis of a reference by Tessmann and Nimuendajú (25a), that the Tikunas employed *yopo*, but since *Piptadenia peregrina* is not known in their area and bearing in mind Schultes' notes on the distribution of *Virola calophylla* and *V. calophylloidea*, I now believe,

even in the absence of botanical specimens, that we may be justified in assuming that they make their narcotic *paricá* from *Virola*. Furthermore, Nimuendajú states that Tikuna snuff is made from the bark of a tree.

Yukuna: linguistic family *Arawak*, according to Koch-Grünberg (22), and Schultes (personal communication).

The Yukunas, who inhabit the uppermost reaches of the Miritiparaná River in the Comisaría del Amazonas, have now almost fully absorbed a once-large tribe of unknown linguistic grouping, the Matapies. The Yukunas are great chewers of coca and employ tobacco-snuff to excess. They use tobacco also in the form of a thick extract and in long cigars, as do their Tukanoan neighbors. *Banisteriopsis* spp. are likewise employed to make a narcotic drink in ways similar to those of adjacent tribes, even though the extent of the employment of this drug is much smaller than that of the Tukanoans to the north (47).

Tanimuka: linguistic family *Arawak*, according to Schultes (personal communication).

The Popeyacá River, affluent of the Apaporis and located near Yukuna country in the Comisaría del Amazonas, is the present center of a Tanimuka population which is small. A split group of Tanimukas early in the present century fled to the distant headwaters of the Igarapé Peritomé, a small tributary of the Apaporis upstream from the Popeyacá, to escape persecution by rubber workers

The Tanimukas use coca, tobacco and *yajé* in exactly the same way as do their neighbors, the Yukunas. The Peritomé-Tanimukas prepare their coca in a very exclusive and wholly distinct form from any other Indians of the Andes or Amazon.

In 1957, Schultes (46) published a note on their novel formula. Powdered coca and its accompanying ashes are treated with smoke from the burning resin of *Protium heptaphyllum* by means of long tubes through which the smoke is blown into the center of a pile of coca-powder. A resinous, aromatic savour is thus given to the coca which greatly improves its taste. This method is an astonishing refinement in coca-preparation and gives cause to wonder whether the Amazon Indians acquired coca in pre-Hispanic days, since this refinement was not mentioned in the Spanish chronicles nor by the Colonial writers nor by subsequent travellers and naturalists. It is also true that these peoples are next to unknown and that few modern naturalists and no earlier chroniclers ever got into their area. Here is most certainly a good case for independent invention, and probably a recent one, since the main group of Tanimukas in the Popeyacá still prepare coca following the general Amazonian method. They sometimes, however, journey for several days to the Peritomé to buy the incensed coca for special occasions from their separated brethren.

Maku: linguistic family or families undetermined, according to Schultes (personal communication). Cf. the classification of Koch-Grünberg (22).

In the little-known forests between the lower Apaporis and Vaupés Rivers of Colombia and in adjacent Brazil, there live groups of nomadic Indians collectively called *Makus*. There appear to be a number of distinct languages involved, at least one of which has been thought, perhaps on superficial evidence, to be remotely related to Puinave. The Makus, who practice no agriculture, have no canoes, build no houses and use no clothing, are extremely primitive in all respects. Some individuals have been enslaved for manual labor by the strong Tukanoan tribes.

Little is known of the Makus. We do know that, as nomadic forest-dwellers, they have a keen knowledge of plants: they acquire machetes from Indian groups of higher culture by preparing for barter a type of curare or arrow-poison which has the reputation of being the best of the entire region. Schultes, who has contacted several groups of Makus, states that, since they cultivate no plants, they chew coca and use tobacco only when visiting settled Indians of other tribes but that they apparently do use *caapi* from wild sources. On the Colombo-Brazilian boundary, Schultes (47) discovered amongst a group of Makus, and experimented with, a new kind of *caapi*, made from *Tetrapterys methystica*, a genus related to *Banisteriopsis*. It is a narcotic prepared from wild lianas and is apparently not cultivated. We have no knowledge as to whether this *caapi* is used only by the Makus or not, but it has not yet been detected amongst the Tukanos.

Karihona: linguistic family *Karib*, according to Mason (24a).

At the present time, there are two isolated groups of Karihonas; one at the headwaters of the Vaupés River, the other in and near La Pedrera on the Brazilian frontier of the Caquetá River. These two groups migrated to their present sites about 1914 from the distant headwaters of the Apaporis River, where they had an internecine war and were decimated by small-pox brought in by white balata-explorers.

They use *yajé* and tobacco, the former as a concentrated drink, the latter as a snuff.

Tunebo: linguistic family *Chibcha*, according to Rivet (38b).

Inhabitants of the humid jungle regions in the south-

western part of the Comisaría de Arauca, still a very poorly known area, the Tunebos are best understood through the works, partly unpublished, of Padre Henri J. Rocheraux (39). The tribe, which to-day is very reduced in size, preserves many primitive customs. They use coca as well as *yopo*. Fresh coca-leaves are toasted but not pulverized. Upon chewing, the leaves are mixed with lime. This is a purely Andean culture-trait. The custom of snuffing *yopo* was acquired probably from their Arawak neighbors in Venezuela and Colombia, for we have information about Tunebo movements to and from various points in southern Venezuela and northwestern Colombia. The Tunebos, according to Rocheraux (39), employ tobacco in the form of a masticatory, using air-dried leaves. A quid is made of these and is chewed. Formerly they did not smoke but recently they have learned this habit from contact with the white man.

Various tribes. Finally, we must consider some tribes located between the Meta and Inirida Rivers, most of which belong to the Arawak and Guahibo linguistic families. The tribes in question are the Puinaves (24), Piapocos (24a), Guayaberos (according to Meden, personal communication) and Guahibos, Kuivas, Amoruas, Sikuanis, Salivas (30) and Kuripakos, according to Schultes (personal communication).

All of these use or were formerly acquainted with *yopo*, especially for purposes of magic. *Yopo*, prepared from the toasted and pulverized seeds of *Piptadenia peregrina*, is normally taken only by the men, for there exists a certain taboo which, however, does not now seem to be so strict as it once was. In the most acculturated of these people, both sexes take it. Snuffing of this violent intoxicant, which looks rather like ground coffee, is carried out with very different kinds of instruments, the most

generally used of which is a double Y-shaped tube of bird bones (the arms of the Y being soldered into place with pitch) ending in two hollowed palm-nuts. These nuts are placed at the opening of the nostrils, and the powder is inhaled from the palm of the hand. Another kind is the long V-shaped snuffing tube, one leg of which is inserted into a nostril, the other into the mouth, thus making self-administration possible. There are additional types of snuffing-tubes as well, both of bone and of small bamboo-like grasses. One other primitive type is made of a palm-leaf: the apex of the leaf is cut off truncated, and this funnel-shaped end is placed over the snuff, while the snuffer draws in strongly through the petiole which is bound into a tube (30, 55).

Generally, some kind of wooden mortar and pestle is used to grind the *Piptadenia*-seeds which have previously been roasted in the fire. The powder is kept in a case made of the leg-bone of the jaguar, partly closed with wax and adorned with feathers. The addition of an alkaline admixture may or may not be the practice.

This narcotic is employed, especially by shamans, for the hallucinogenic effects produced by bufotenine, an active principle believed to be responsible for the startling activity of the intoxication (13).

These tribes of the llanos areas of Colombia likewise take tobacco, usually in the form of large cigars wrapped in very fine maize husks (30).

The Piapoko, Puinave and Guahibo Indians make use of *yajé* but not as a drink. The bark of the root of the vine is simply chewed, and narcotic effects are said thus to be induced.

IV.

In summary, I may say that all that has been attempted in this article is an overall picture of the very extensive use of narcotics and stimulants by the indige-

nous population of Colombia. This is a country highly developed spiritually, intellectually and materially. The use of these plants in the native cultures of a country with such a modern civilization represents, paradoxicallly, a condition far in advance of that usually found where native cultures frequently weaken or disappear. It demonstrates for the indigenous civilizations of Colombia a spiritual power and a cultural balance as well as the existence in the mind of the native of a fixed purpose in his use of narcotics. It is likewise significant and of a value beyond measure for science that we can look in this present age to such a rich knowledge of economic plants by primitive peoples. Here we have at hand the possibility of studying materials *in situ*. For botany, for anthropology and for medicine, Colombia is a seemingly inexhaustible treasure-house.

LITERATURE CITED

1. Bernal V., Segundo, 1954. Magia y Medicina entre los Paéces. Rev. Col. Anthrop. 2: 221–264.
2. Calella P., Plácido de, 1945. Tabaco entre las tribus Siona. Amazon. Col. American. 3: 39.
3. Castellví, Marcelino de, 1934. Las investigaciones linguísticas, para uso de los investigadores del Departamento de Nariño y de las regiones del Caquetá, Putumayo y Amazonas.
4. ——, 1938. La lengua Kofán. Journ. Soc. Amer. Paris, n.s. 30: 219–233.
5. ——, 1939. Bibliografía sobre la familia linguística Tukano. Proc. Second Conv. Inter-Amer. Libr. Assoc. Amer. ser. 2, 2.
6. ——, 1941–44. Materiales etnobotánicos sobre el tabaco y la coca. Rev. Amazon. Col. American. 2, nos. 4–6.
7. ——, 1953. La Macrofamilia linguística Witoto. Rev. Amazon. Col. American. 5: nos. 17–19.
8. Claes, Florent, 1932–34. Chez les indies Correguajes. Bull. Soc. Roy. Belgue de Geogr. nos. 56–58, 27–51.
9. De Alviano F., Fidelis, 1953. Noticia Etnográfica dos Indios Ticunas. Miscelánea Padre Castellví, 129.
10. De la Rosa, Alférez, José Nicolas, 1949. Floresta de la Santa Iglesia Catedral de Santa Marta [copy], 279.
11. Duque Gómez, Luis, 1945. Misiones de estudio. Bol. Arqu. 1: 215.
12. Dupuoy, Walter, 1952. Aspectos folklóricos del uso del Chimo. Arch. Venez. Folkl. 2: 3–12.
13. Fabing, Howard D., 1956. Bufotenina (E) Yopo — On Going Beserk: A Neurochemical Inquiry. Sci. Month. 83, no. 5.
14. Frazer, Sir James George, 1923. The Golden Bough, 11–12.
14a. Fúlop, Marcos, 1954. Aspectos de la cultura Tucano. Cosmog. Rev. Col. Antrop. 3: 99–137.
15. Gentner, Walter A., 1954. The Genus Erythroxylum in Colombia. [Ms. inéd.] Bogotá.
16. Goodspeed, Thomas H., 1954. The Genus Nicotiana, 19–36.
17. Holmer, Nils M., 1952. Contribución a la linguística de la Sierra Nevada. Rev. Col. Antrop. 1: 313.
18. Igualada, Bartolomé de, 1938. Tres emocionantes exploraciones misionales por el río Cahuinarí. Bol. Estud. Hist. 7, no. 83.

18a. Jijón y Caamaño, Jacinto, 1939. Materiales para el mapa linguistico del Occidente de Colombia. Bol. Estud. Hist. Pasto 12: 167–175.
19. Julián, Antonio, 1949. La Perla de América y Provincia de Santa Marta [copy]. Discurso VI.
20. Koch-Grünberg, Theodor, 1906. Les Indiens Ouitotos. Journ. Soc. American 3: 157–189.
21. ——, 1923. Zwei Jahre bei den Indianern Nordwest-Brasiliens, 34, 85.
22. ——, 1917. Von Roroima zum Orinoco 1: map. 407.
23. Levy-Bruhl, Lucien, 1922. La Mentalité Primitive, 47–50.
24. Loukotka, Cestmir, 1935. Clasificación de las lenguas sudamericanas. Edicion "Linguística sudamericana," no. 1.
24a. Mason, John Alden, 1950. The Language of South American Indians 6: 157–317.
25. Monconil, Gaspar M., 1945. Preparación del tabaco entre los Witoto. Rev. Amazon. 3: nos. 9–10.
25a. Nimuendaju, Curt, 1952. Am. Arch. Ethnol. 45: 23, 79, 101, 104.
26. Ortíz, Sergio Elías, 1937. Clasificación de las lenguas indígenas de Colombia. Idearium 1.
26a. ——, 1943. Familia Witoto. Rev. Hist. Pasto 9.
26b. ——, 1954. Linguística Aborigen de Colombia, 161–187, 209–247, 247–271, 271–349, 349–373, 413.
27. Pardal, Ramón, 1937. Medicina Aborigen Americana 32.
28. Pineda, Roberto, 1947. Aspectos de la Magia en la Guajira. Rev. Inst. Etnol. Nal. 3: 11.
29. Preuss, Konrad T., 1921. Religion und Mythologie der Uitoto, 219, 234, 254.
30. Reichel-Dolmatoff, Gerard, 1944. La cultura de los Indios Guahibo. Rev. Inst. Etnol. Nal., 435–454.
31. ——, 1946. Etnografía Chimila. Bol. Arqu. no. 2, 98–146.
32. ——, 1946. Informe sobre las investigaciones preliminares de la Comisión Etnológica al Catatumbo. Bol. Arqu., no. 4, 392.
33. ——, 1945. Los Indios Motilones. Rev. Inst. Etnol. Nal. 7: 18, 26, 33, 54.
34. ——, 1945. Cilomanufactura de la serámica entre los Chamí. Bol. Arqu. 1: 429.
35. ——, Gerard y Alicia, 1944. Grupos sanguíneos entre los indios Pijao del Tolima. Rev. Inst. Etnol. Nal., 507.
36. Reichel-Dolmatoff, Gerard, 1949. Los Kogi. Rev. Inst. Etnol. Nal., T.I.V. IV, 1.
37. ——, 1951. Los Kogi. Una tribu de la Sierra Nevada de Santa Marta. T II. Bogota.

38. Rivet, Paul, 1924. Langues Americaines III. Langues de l'Amerique du Sud et des Antilles. In Meillet, A. and Cohen, Marcel, "Les Langues du Monde," Coll. Ling. Paris 16: 629–715.
38a. ——, 1943. La lengua Chocó. Rev. Inst. Etnol. Nac., 131–196; 1944, 297–349.
38b. ——, 1943. La lengua Tunebo. Rev. Inst. Etnol. Nac., 47–53.
39. Rocheraux, Henri J. Les Unkasias. [Ms. ined.]
39a. Rondon, Frederico, 1945. Uaupés.
40. Safford, William E., 1920. Daturas of the Old World and New: an account of their narcotic properties and their use in oracular and initiatory ceremonies. Ann. Rept. Smithson. Inst. 561–567.
41. Seemann, Berthold, 1852–1857. The Botany of the voyage of the H.M.S. Herald. London, 68–69.
42. Schultes, Richard Evans, 1945. El uso del Tabaco entre los Huitotos. Agricult. Trop. no. 9, 19–22.
43. ——, 1954. Un nouveau tabac à priser de L'Amazone du Nord-Ouest, 1954. Journ. Agric. Trop. Bot. Appl., 298–311.
43a. ——, 1954. A new narcotic snuff from the northwest Amazon. Bot. Mus. Leafl. Harvard Univ. 16: 241–260.
44. ——, 1955. A new narcotic genus from the Amazon slope of the Colombian Andes. Bot. Mus. Leafl. Harvard Univ. 17: 1–11.
45. ——, 1942. Plantae Colombianae II: Yoco: a stimulant of southern Colombia. Bot. Mus. Leafl. Harvard Univ. 10: 301–322.
46. ——, 1957. A new method of coca preparation in the Colombian Amazon. Bot. Mus. Leafl. Harvard Univ. 17: 241–264.
47. ——, 1957. The identity of the malpighiaceous narcotics of South America. Bot. Mus. Leafl. Harvard Univ. 18: 1–56.
48. Taylor, E. B., 1903. Primitive culture researches into the development of mythology, philosophy, religion, art and custom.
49. Tessmann, Günter, 1930. Die Indianer Nordost-Perus, 319.
50. Uscátegui M., Nestor, 1954. Contribución al estudio de la masticación de las hojas de coca. Rev. Col. Antrop. 3: 209–289.
51. ——, 1956. El tabaco entre las tribus indígenas de Colombia. Rev. Col. Antrop. 5: 12, 52.
52. ——. Función social de los narcóticos y estimulantes en las tribus indígenas de Colombia. [Ms. inéd.]
53. Vinalesa, José de, 1952. Indios Arhuacos. Rev. Inst. Etnol. 5.
54. Wassen, Henry, 1935. Notes on southern groups of Chocó Indians in Colombia. Ethnol. Stud. 1–3, 101–102.
55. Wurdack, J. J., 1958. Indian narcotics in southern Venezuela. Gard. Journ., 116–118.

PLANTAE COLOMBIANAE XV

PLANTAE NOVAE COLOMBIANAE ORIENTALIS DESCRIPTIONES

BY

RICHARD EVANS SCHULTES

OUR continued investigation of recently collected Colombian plants, especially those from the northwesternmost part of the Amazon Valley, has brought to light several species hitherto apparently undescribed. Descriptions of these concepts are offered in the present paper.

Gratefully I acknowledge the artistry of Mr. Johann Gumppenberg who has made the line-drawings published herein. My thanks are due also to the National Science Foundation for a grant which made possible the drawings and their publication.

CYCLANTHACEAE

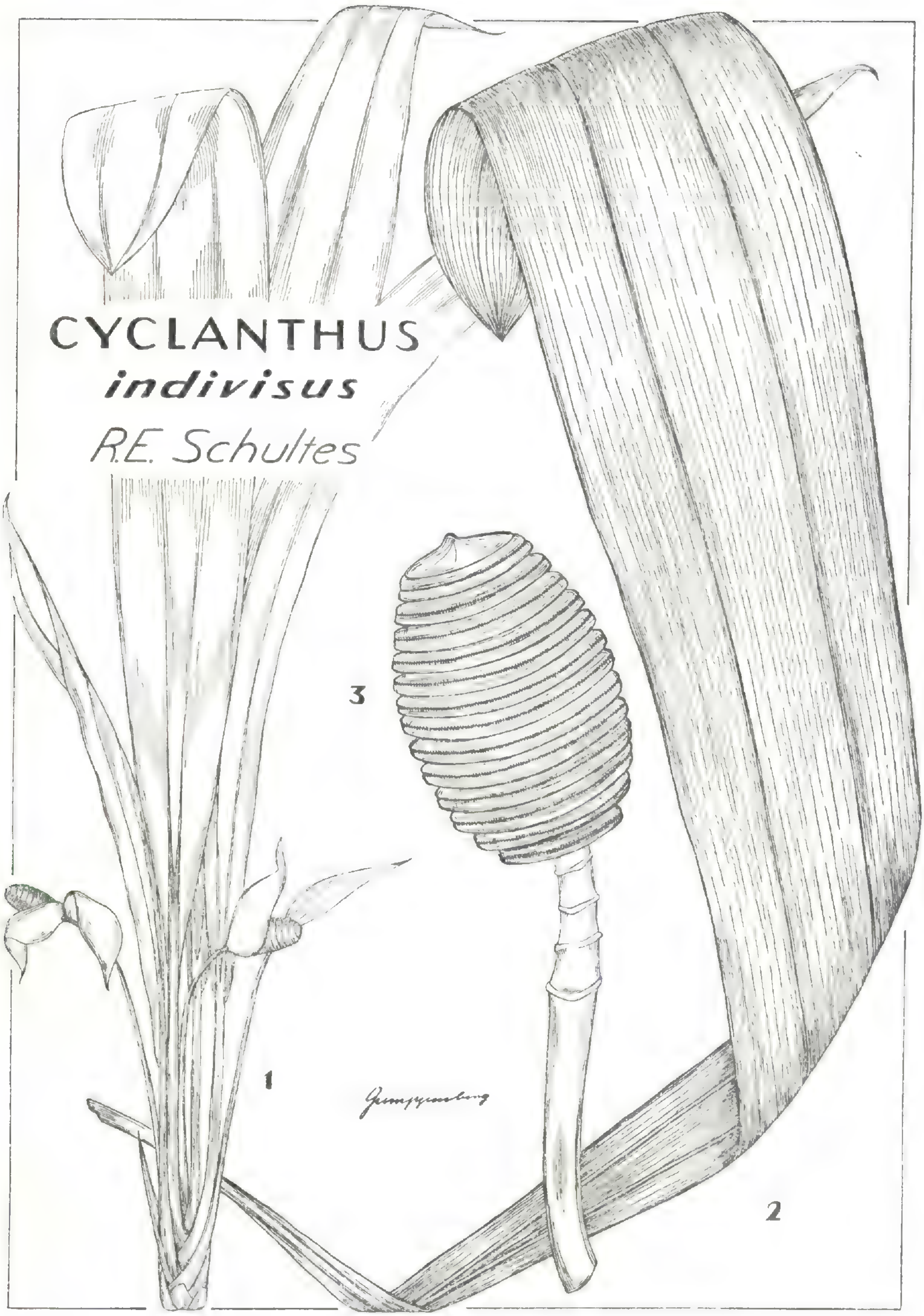
Cyclanthus indivisus *R. E. Schultes sp. nov.*

Planta terrestris, acaulescens, usque ad 130 cm. alta. Petiolus 30–40 cm. longus vel brevior, leviter angulatus. Lamina tenuiter sed firme chartacea, concoloria, integra (non bifida), oblanceolata, 90–115 cm. longa, 10–15 cm. lata, apice acuminata, basi sensim acuminata, bicostata, robustis cum nervis principalibus stramineis, nervulis parallellibus plusminusve quattuorviginta. Inflorescentiae axis atropurpureus, teres, aliquid carnosus, 30–45 cm. longus, 0.6–10 mm. in diametro. Spathae quattuor, exteriores extus virides sed intus flavae, interiores utrinque flavae apicem versus rubrae. Spadix breviter et late cylindricus, 6–7 cm. longus, 25–45 mm. in diametro, ma-

EXPLANATION OF THE ILLUSTRATION

PLATE LVIII. CYCLANTHUS INDIVISUS *R. E. Schultes.* 1, habit drawing of plant, approximately one eighth natural size. 2, mature leaf, approximately one quarter natural size. 3, spadix, approximately three quarters natural size.

Drawn by JOHN GUMPPENBERG


CYCLANTHUS
indivisus
R.E. Schultes
3
1
2

EXPLANATION OF THE ILLUSTRATION

PLATE LIX. Habit photograph of CYCLANTHUS INDIVISUS *R. E. Schultes* at Soratama, Río Apaporis, Amazonas, Colombia.

Photograph by RICHARD EVANS SCHULTES

Plate LIX

turitate purpureus vel atrorubrus, flavis cum florium cinctis. Flores vanilli-fragrantes, valde eis *Cyclanthi bipartiti* similes sed staminibus multo majoribus.

Cyclanthus indivisus grows together with the widespread *C. bipartitus* Poir., but it is easily distinguished in the field by its usually much smaller size, its entire leaf-blades and its shorter and stouter spadix. The ripened spadix in *Cyclanthus bipartitus* is commonly about eight times as long as its diameter; that of *C. indivisus* in length apparently never measures more than five times its diameter and may often be shorter. In the former species, the spadix is most often entirely whitish yellow; in the latter, it is a beautiful purple-red with yellow bands of flowers.

Colombia: Comisarías del Amazonas y Vaupés, Rio Apaporis, Soratama (entre el Río Pacoa y el Río Kananarí). "Growing out of ground directly. Fruiting stalk purple. Outer bract green outside, yellow inside. Inner bract yellow inside, red towards tip. Latex (!) white. On floodland." August 20, 1951, *Richard Evans Schultes & Isidoro Cabrera 13680* (Type in Herb. Gray).

Anthurium polyschistum *R. E. Schultes & Idrobo sp. nov.*

Planta epiphytica. Caudex scandens, circiter 0.7 cm. in diametro, internodiis plusminusve 8 cm. longis. Cataphylla coriacea, 3 cm. longa, persistentia. Petiolus teretiusculus, leviter sulcatus, apice breviter geniculatus, lamina plusminusve aequalis, 20–23 cm. longus. Folia membranacea, laete viridis, profundissime 12–15-secta, segmentis anguste lanceolato-ensiformibus, apice acuminatis, basi sensim attenuatis, petiolulo brevissimo, ad 20 cm. longis, 1–2 cm. latis, nervo collectivo a margine 1–2 mm. remoto et nervo centrali siccitate stramineo robusto. Pedunculus 25 cm. longus vel longior. Spatha albido-viridis, elongato-lanceolata, apice acutissima, usque ad

12 cm. longa, basi 1–1.3 cm. lata. Spadix apparenter sessilis, cylindricus, usque ad 10 cm. longus. Tepala interna pallida. Staminum filamenta alba; antherae flavae. Ovarium viride, oblongum. Fructus adhuc ignotus.

Anthurium polyschistum appears to be nearest to the poorly understood *A. eminens* Schott. It differs, however, in being a crawling epiphyte, not an "arborescent" plant, in having much smaller leaves, a much shorter petiole, a spadix only one-fifth as long, and in the color of the spathe. *Anthurium polyschistum* is, in general, a much weaker and smaller plant.

COLOMBIA: Comisaría del Amazonas, Trapecio amazónico, Amazon River watershed. Loretoyacu River. Alt. about 100 m. March 1946, *Richard Evans Schultes 7179* (TYPE in U.S. Nat. Herb. 1996025).

Urospatha antisylleptica *R. E. Schultes sp. nov.*

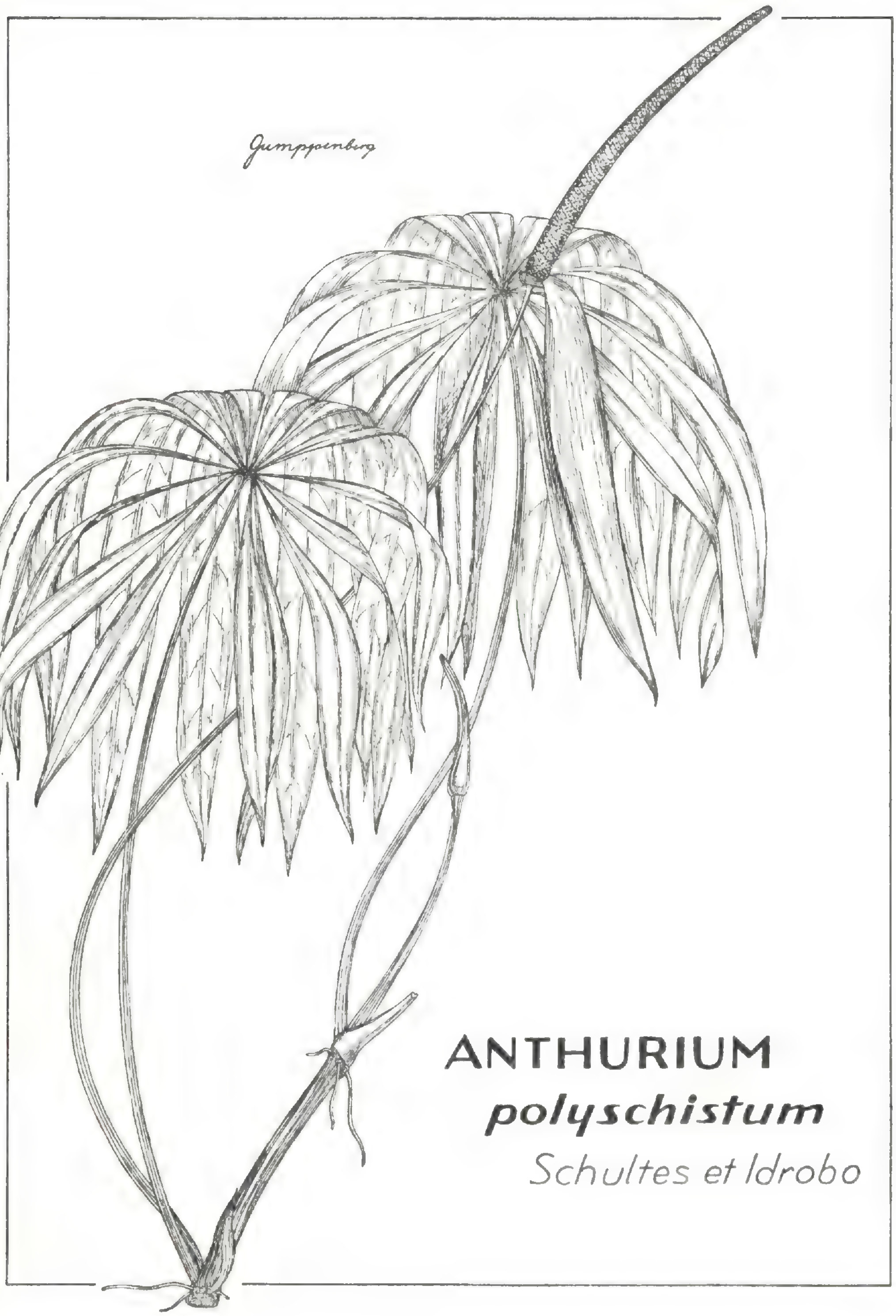
Herba silvatica paludosaque, usque ad sex ped. alta. Foliorum petiolus succulentus, comparate tenuis, glabrus, leviter striatus, atroviridis maculis cinereo-viridibus et atropurpureus variegatus, usque ad 150 cm. longus; lamina hastata, statu adulta usque ad 80 cm. longa; lobus anticus lanceolatus, usque ad 47 cm. longus, basi 13 cm. latus, basi (petioli apicem versus) callo valde atrosanguineo conspicuoque; postici late lanceolati, illi subaequilongi, parte latiore usque ad 14 cm. lati; lateralibus primariis lobi antici subconspicuis angulo acutissimo 15–20° adscendentibus, infimis interlobariis costae posticae breviter adnatis, bicruribus, superioribus duo in lobi parte apicali exeuntibus; costis posticis in sinu longe (5 cm.) denudatis. Pedunculus petiolis sed gracilior glabrus, similiter variegatus, usque ad plusminusve 115 cm. longus, cum spatha foliis multo brevior. Spatha aperta spiraliter contorta, elongato-lanceolata, longissime acuminata, extus viridi-purpurea, intus pallide viridia sed basim versus rosea, usque ad plusminusve 33 cm. longa. Spadix ses-

EXPLANATION OF THE ILLUSTRATION

PLATE LX. ANTHURIUM POLYSCHISTUM *R. E. Schultes & Idrobo.* Habit drawing approximately one half natural size.

Drawn by JOHN GUMPPENBERG

Plate LX



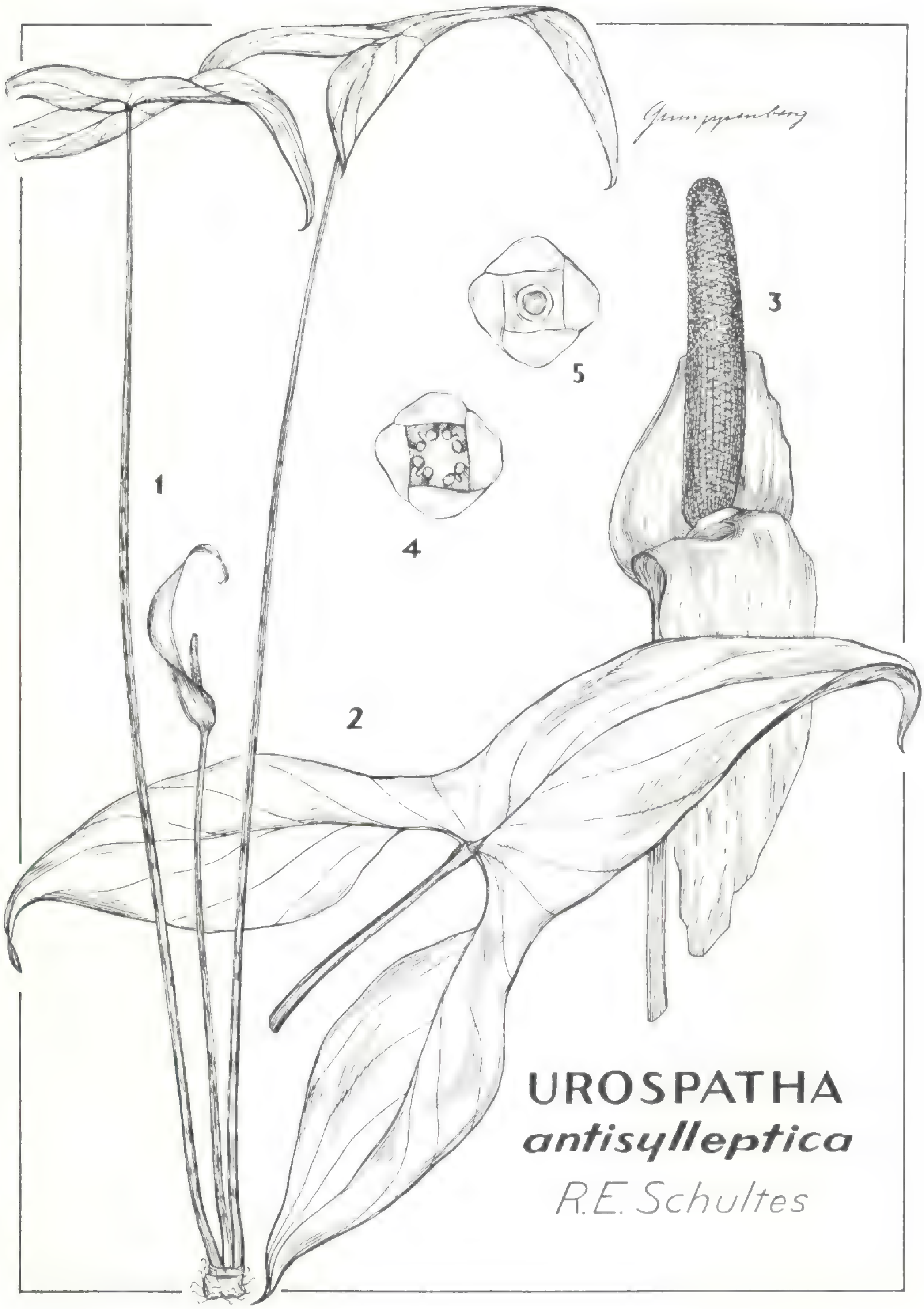
ANTHURIUM
polyschistum
Schultes et Idrobo

EXPLANATION OF THE ILLUSTRATION

PLATE LXI. UROSPATHA ANTISYLLEPTICA *R. E. Schultes.* 1, habit drawing, approximately one fourteenth natural size. 2, mature leaf approximately one sixth natural size. 3, inflorescence with spathe partially removed to show sessile spadix, approximately three quarters natural size. 4 and 5, aspects of flower and ovary, approximately ten times natural size.

Drawn by JOHN GUMPPENBERG

Plate LXI



UROSPATHA
antisylleptica
R.E. Schultes

silia (non stipitatus), perfecte cylindricus, apice rotundatus, rufo-brunneus; spathae parte inferiore breviter adnatus, circiter 5.5 cm. longus, 1 cm. in diametro, a medio fertiles. Flores quattuor-tepali, virides. Ovarii obovoidei, loculi quattuor-ovulati. Baccae seminaque adhuc ignoti.

Urospatha antisylleptica differs from *U. deeipiens* primarily in being much larger and in having the sinus between the median and lateral lobes of the leaf at least twice as long. From *Urospatha Hostmanii*, the new species may be distinguished by its larger size, by its verruculose (not glabrous) petioles and by its having the base of the spathe only very shortly adnate to the spadix.

The bright blood-red or scarlet callus at the base of the leaf blade or apex of the petiole in *Urospatha antisylleptica* may be a distinguishing feature from all other species, for I have seen no reference to such a color in the literature nor have I noticed it in several other species of this genus which I have had occasion to study and collect in the field.

Urospatha antisylleptica was pointed out independently by two Barasana Indians, who inhabit the upper course of the Río Piraparaná and its affluents, as the source of an oral contraceptive which is in common use in the tribe. They report that the unripened spadix is dried and pulverized and that, in order to prevent conception, the resulting brown powder is added to food given to any woman. My stay in the Río Piraparaná was not long enough to permit me to check these statements thoroughly or to see the plant used. Since the two sources of this information were independent of each other and since species of the *Araceae* are said to be similarly used in other parts of the Vaupés and elsewhere, I am inclined to give credence to the reports. The specific name *antisylleptica* (from the Greek meaning "against pregnancy") has been chosen to call attention to this unusual use of the plant.

COLOMBIA: Comisaría del Vaupés, Río Piraparaná (tributary of Río Apaporis). Headwaters of Caño Teemeeña. "In water. Stem mottled black and grey-green. Spathe spiralled, outside purple-green, inside basally pink, above green-brown. Callus at base of leaf bright red. Height 6 feet." September 10, 1952, *Richard Evans Schultes & Isidoro Cabrera 17425* (TYPE in Herb. Gray).

OCHNACEAE

Rhytidanthera regalis *R. E. Schultes* in Bot. Mus. Leafl. Harvard Univ. 16 (1953) 106, t. 18.

When this beautiful tree was described, a habit photograph was published. Inasmuch as it is well to illustrate as many novelties as possible with a drawing or a detailed photograph, the accompanying line-drawing of *Rhytidanthera regalis* is hereby offered.

APOCYNACEAE

Tabernaemontana rimulosa *Woodson ex R. E. Schultes* in Bot. Mus. Leafl. Harvard Univ. 18 (1958) 180; *sine specimine designatione.*

Through an editorial oversight, no type specimen was cited for the description of this concept. In the International Code of Botanical Nomenclature (1956), Article 35 stipulates that "publication on or after 1 Jan. 1958 of the name of a new taxon of recent plants of the rank of order or below is valid only when the nomenclatural type is indicated." In order to validate Woodson's publication, we hereby print the essensial data which was previously omitted. It is my understanding that this binomial, since it was not validly published, must date from the present article.

The type and only known collection of *Tabernaemontana rimulosa* is the following:

COLOMBIA: Comisaría del Vaupés, Río Negro, San Felipe and vicinity (below confluence of Río Guainía and Río Casiquiare). Altitude about 600 feet. General location: Lat. 1°50′ N, Long. 67°0′ W. October 25, 1952. *Richard Evans Schultes, Richard E. D. Baker & Isidoro Cabrera 17983* (TYPE in Mo. Bot. Gard.).

EXPLANATION OF THE ILLUSTRATION

PLATE LXII. RHYTIDANTHERA REGALIS *R. E. Schultes.* 1, branch with leaves and flowers, approximately one half natural size. 2, fruits, approximately one half natural size. 3, flower, approximately one and one quarter natural size. 4, sepal, approximately one and one half natural size. 5, stamen, approximately seven times natural size; apical part of stamen showing pores, approximately thirty times natural size.

Drawn by JOHN GUMPPENBERG

Plate LXII

RHYTIDANTHERA

regalis

R.E. Schultes

ON THE VALIDITY OF THE GENERIC NAME *COCHLEANTHES* RAF.

BY

RICHARD EVANS SCHULTES AND LESLIE A. GARAY

THE orchid genus which is known as *Warscewiczella* Rchb.f. appears to be worthy of recognition, but the validity of this name is open to serious doubt. We consider that the genus is closely related to *Chondrorhyncha* of the *Huntleyinae*, but many of the species which properly belong to *Warscewiczella* have been referred to various genera of the *Zygopetalinae*. The entire *Huntleya-Zygopetalum* alliance is in need of a critical study. It is, however, essential to clarify some of the nomenclatorial problems prior to the undertaking of such a study, and a start in this direction has been made in the present paper.

Reichenbach established the genus *Warscewiczella* in 1852, basing his concept on *Warrea discolor* Lindl., and pointing out its relationship to *Warrea* and *Chondrorhyncha*. In 1836, Lindley had described, as *Zygopetalum cochleare*, a plant from Trinidad which cannot be accommodated in *Zygopetalum* as now interpreted, but which conforms with Reichenbach's *Warscewiczella*. In the same year, Rafinesque indicated that Lindley's *Zygopetalum cochleare* represented a distinct genus which he called, quite appropriately, *Cochleanthes*, citing as type "*Zygopetalum cochleare* Lindl. b. reg. 1857" and stating that it was "quite a different G. from *Z. makai* H. b. m.

2748." Rafinesque proposed for Lindley's *Zygopetalum cochleare* a new specific name under *Cochleanthes* — *C. fragrans* — instead of making the correct transfer.

There is every reason to accept *Cochleanthes* as the proper name for this generic concept, even though it has been almost completely neglected[1] in orchidological literature. Under the International Code of Botanical Nomenclature, the only way to avoid a change to *Cochleanthes* would be to conserve *Warscewiczella*. This procedure we are not willing to propose, since the genus is a small one and since none of the species involved has ever assumed important stature in horticulture.

Cochleanthes *Rafinesque* Fl. Tellur. 4 (1836) 45.
Warscewiczella Rchb.f. in Bot. Zeit. 10 (1852) 635.
Zygopetalum sect. *Cochleare* Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 652.
Zygopetalum sect. *Warscewiczella* Rchb.f. ibid. 6 (1863) 653.

ORIGINAL DESCRIPTION:

930. **Cochleanthes** *R.* (shell fl.) petalis connivens ovat. undul. lab. cochleato bilobo, basi crista cochleata (ut plecton plicata) calcar col. clavata, anth. 2loc., 2labiata, pollinia 4eq. *caulescens, fl. axillaris.*—Type *C. fragrans* R. fol. lanceol. 5nervis, pedic. lfl. axillaris. Trinidad. fl. ample fragrant white, lip purple. It is Zygopetalum cochleare Lindl. b. reg. 1857, but quite a different G. from Z. makai H. b. m. 2748, with petals secund, lip flabellate with a spur, anther calciform, 4 uneq. pollen."

Cochleanthes amazonica (*Rchb.f. & Warsc.*) *R.E. Schultes & Garay comb. nov.*

Warscewiczella amazonica Rchb.f. & Warsc. in Bonpl. 2 (1854) 97.

[1] Hoehne (in Hoehne, Fl. Brasilica 12: pt. 7 (1953) 171), in referring to "*Cochleanthus* Rafin.", has pointed out that this is the prior name, but, for reasons not explained, he continued to employ *Warscewiczella*.

Zygopetalum amazonicum (Rchb.f. & Warsc.) Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 655.
Warscewiczella Lindeni Hort. in Journ. Hort. 1 (1892) 449.
Zygopetalum Lindeni (Hort.) Rolfe in Lindenia 8 (1892) 5, t. 337.

Cochleanthes aromatica (*Rchb.f.*) *R. E. Schultes & Garay comb. nov.*
Zygopetalum aromaticum Rchb.f. in Bot. Zeit. 10 (1852) 668.
Warscewiczella aromatica (Rchb.f.) Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 654.
Zygopetalum Wendlandi Rchb.f. in Beitr. Orch. Centr.-Amer. (1866) 74.
Bollea Wendlandiana Hort. ex Gard. & For. 1 (1888) 315.
Warscewiczella Wendlandi (Rchb.f.) Schltr. in Beih. Bot. Centralbl. 36, pt. 2 (1918) 494.
Chondrorhyncha aromatica (Rchb.f.) P. H. Allen in Ann. Missouri Bot. Gard. 36 (1949) 85.

Cochleanthes bidentata (*Rchb.f. ex Hemsl.*) *R. E. Schultes & Gary comb. nov.*
Zygopetalum bidentatum Rchb.f. ex Hemsl. in Salvin Biol. Centr. Amer. 3 (1885) 251.
Warscewiczella bidentata (Rchb.f. ex Hemsl.) Schltr. in Beih. Bot. Centralbl. 36, pt. 2 (1918) 494.

Cochleanthes candida (*Lindl.*) *R. E. Schultes & Garay comb. nov.*
Warrea candida Lindl. in Paxt. Fl. Gard. 1 (1851) 32, fig. 22.
Huntleya candida Hort. ex Lindl. loc. cit., *in synon.*
Zygopetalum candidum (Lindl.) Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 656.

Cochleanthes digitata (*Lehm.*) *R. E. Schultes & Garay comb. nov.*

Warrea digitata Lemaire in Illustr. Horticol. 3 (1856) Misc. p. 70.

Huntleya imbricata Pinel. ex Lem. in Illustr. Horticol. 4 (1857) sub t. 152, *in synon.*

Warscewiczella digitata Barb.-Rodr. Struct. des Orchid. (1883) t. 13, fig. 3.

Cochleanthes discolor (*Lindl.*) *R. E. Schultes & Garay comb. nov.*

Warrea discolor Lindl. in Journ. Hort. Soc. Lond. 4 (1849) 265.

Warscewiczella discolor (Lindl.) Rchb.f. in Bot. Zeit. 10 (1832) 636.

Zygopetalum discolor (Lindl.) Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 655.

Chondrorhyncha discolor (Lindl.) P. H. Allen in Ann. Missouri Bot. Gard. 36 (1949) 87.

Cochleanthes flabelliformis (*Sw.*) *R. E. Schultes & Garay comb. nov.*

Epidendrum flabelliforme Sw. Prodr. (1788) 123.

Cymbidium flabelliforme (Sw.) Sw. in Nov. Act. Ups. 6 (1799) 73.

Cochleanthes fragrans Raf. Fl. Tellur. 4 (1836) 45.

Zygopetalum cochleare Lindl. in Bot. Reg. 22 (1836) t. 1857.

Eulophia cochleata Knight ex Hooker in Bot. Mag. 64 (1837) sub t. 3585, *in synon.*

Zygopetalum cochleatum Paxton Magaz. Bot. 4 (1838) 279.

Eulophia cochlearis (Lindl.) Steudel Nom., ed. 2, 1 (1840) 605.

Warscewiczella cochlearis (Lindl.) Rchb.f. in Bot. Zeit. 10 (1852) 714.

Huntleya imbricata Hort. ex Rchb.f. ibid., *in synon.*
Zygopetalum flabelliforme (Sw.) Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 652.
Zygopetalum conchaceum Hoffmansegg ex Rchb.f. ibid., *in synon.*
Cymbidium flabellifolium Sw. ex Griseb. Fl. Brit. West Ind. Isl. (1864) 629, *in synon.*
Warscewiczella cochleata Barb. Rod. Struct. des Orchid. (1883) t. 13, fig. 4.
Zygopetalum Gibeziae N. E. Brown in Lindenia 4 (1888) 79, t. 181.
Warscewiczella Gibeziae (N. E. Brown) Stein Orchideenb. (1892) 595.
Warscewiczella flabelliformis (Sw.) Cogn. in Urban Symb. Antill. 4 (1903) 182.

Cochleanthes heteroclita (*Poepp. & Endl.*) *R.E. Schultes & Garay comb. nov.*
Maxillaria heteroclita Poepp. & Endl. Nov. Gen. ac Sp. 1 (1836) 37, t. 63.
Zygopetalum rhombilabium C. Schweinf. in Amer. Orch. Soc. Bull. 12 (1944) 422.
Warscewiczella heteroclita (Poepp. & Endl.) Hoehne in Arq. Bot. Est. S. Paulo, nov. ser., 2, pt. 6 (1952) 126.

Cochleanthes ionoleuca (*Rchb.f.*) *R. E. Schultes & Garay comb. nov.*
Zygopetalum ionoleucum Rchb.f. in Bot. Zeit. 23 (1865) 99.
Warscewiczella ionoleuca (Rchb.f.) Schltr. in Fedde Rep. Beih. 7 (1920) 267.

Cochleanthes Klugii (*C. Schweinf.*) *R. E. Schultes & Garay comb. nov.*

Zygopetalum Klugii C. Schweinf. in Bot. Mus. Leafl. Harvard Univ. 15 (1952) 150.

Cochleanthes Lueddemanniana (*Rchb.f.*) *R. E. Schultes & Garay comb. nov.*

Warscewiczella Lueddemanniana Rchb.f. in Hamb. Gartenzeit. 16 (1860) 179.

Zygopetalum Lueddemannianum (Rchb.f.) Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 653.

Cochleanthes marginata (*Rchb.f.*) *R. E. Schultes & Garay comb. nov.*

Warscewiczella marginata Rchb.f. in Bot. Zeit. 10 (1852) 636.

Huntleya marginata Hort. ex Rchb.f., loc. cit.

Warrea marginata Rchb.f., loc. cit.

Warrea quadrata Lindl. in Gard. Chron. (1853) 647.

Warscewiczella velata Rchb.f. in Bot. Zeit. 23 (1865) 99.

Zygopetalum quadratum Pfitz. Vergl. Morph. Orch. (1881) 58.

Chondrorhyncha Lipsicombiae Rolfe Kew Bull. (1912) 133.

Chondrorhyncha marginata (Rchb.f.) P. H. Allen in Ann. Missouri Bot. Gard. 36 (1949) 88.

Cochleanthes trinitatis (*Ames*) *R. E. Schultes & Garay comb. nov.*

Zygopetalum trinitatis Ames Sched. Orchid. 3 (1923) 21.

Cochleanthes Wailesiana (*Lindl.*) *R. E. Schultes & Garay comb. nov.*

Warrea Wailesiana Lindl. in Journ. Hort. Soc. 4 (1849) 264.

Zygopetalum Wailesianum (Lindl.) Rchb.f. in Walp. Ann. Bot. Syst. 6 (1863) 656.
Warscewiczella Wailesiana (Lindl.) Rchb.f. ex Morren in Belg. Hort. 28 (1878) 183.

Excluded species

Warscewiczella calloglossa *Schltr.* in Fedde Rep. 12 (1913) 216 = *Chondrorhyncha calloglossa* (Schltr.) P. H. Allen.

Warscewiczella Gehrtiana *Hoehne* in Arq. Bot. Est. S. Paulo, nov. ser., 1, pt. 1 (1945) 5 = *Hochneella Gehrtiana* (Hoehne) Ruschi.

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THE ORIGIN OF CORN

I. POD CORN, THE ANCESTRAL FORM

BY

PAUL C. MANGELSDORF AND ROBERT G. REEVES[1]

IT IS now one hundred years since the first edition of Darwin's epoch-making book "On the Origin of Species" appeared in the London bookstalls. It would be difficult to overestimate the immediate impact of this work, or its continuing influence throughout the ensuing century, not only upon all branches of biology but also upon the other sciences and indeed upon virtually all fields of human thought. It has been said with some degree of truth that "Next to the Bible no work has been quite as influential, in virtually every aspect of human thought, as the 'Origin of Species.' "

To the student of cultivated plants, the book was — and is — of special interest because Darwin's conclusions, arguments and theories were founded, to a large extent, on his monumental studies of domestic animals and cultivated plants. The first chapter in the book is devoted to this subject, and Darwin subsequently wrote a two-volume treatise on the variation of animals and plants under domestication. He believed that the key to the problems of modification and adaptation was to be found in the study of variation of organisms under domestica-

[1] Professor, Departments of Agronomy and Genetics, Texas Agricultural Experiment Station.

tion. A passage in the introduction to "On the Origin of Species" makes this abundantly clear:

> At the commencement of my observations it seemed to me probable that a careful study of domesticated animals and of cultivated plants would offer the best chance of making out this obscure problem. Nor have I been disappointed; in this and in all other perplexing cases I have invariably found that our knowledge, imperfect though it be, of variation under domestication, afforded the best and safest clue. I may venture to express my conviction of the high value of such studies, although they have been very commonly neglected by naturalists.

Darwin's studies on domestic animals and plants, together with those of De Candolle on the origins of cultivated plants, have been the inspiration for our own work, at once more restricted in its scope and more intensive in its treatment, on the origin of Indian corn. It is now twenty years since we proposed the tripartite theory[2] which postulates (A) that cultivated maize originated from a wild form of pod corn which was once indigenous to the lowlands of South America; (B) that teosinte (*Zea mexicana*), the closest relative of maize, is the product of a natural hybridization of Zea and Tripsacum which occurred after cultivated maize had been introduced by man into Central America; (C) that new types of corn originating directly or indirectly from this cross and exhibiting admixture with Tripsacum or teosinte comprise the majority of modern Central American and North American varieties.

During these twenty years, an impressive volume of new research bearing on the problem has been completed, much of it stimulated and guided by the theory itself.

[2] In this paper we, like other students of maize, use the word "theory" in its popular or semipopular meaning. In a strict sense, we are not dealing with theories — certainly not with theories involving broad principles — but with hypotheses. Webster's Dictionary defines hypothesis as "a tentative theory or supposition, provisionally adopted to explain certain facts and to guide in the investigation of others."

During this same period, the theory has also been the object of lively controversy and of strong objections. On this hundredth anniversary of the publication of Darwin's "On the Origin of Species" and the twentieth anniversary of our own more modest contribution, it seems appropriate to take a broad new look at the entire problem of the origin of corn — a problem which not only is fascinating in its own right, but one whose solution promises to shed some light on the evolution of other cultivated species. It is our purpose, then, to evaluate both the old and the new evidence as well as the objections; to consider the various theories which have been proposed; and to review the extensive relevant literature which has appeared in the last two decades.

In discussing theories on the origin and evolution of maize, it is perhaps inevitable that we should give major attention to our own. There is nothing unusual in this situation. Most new theories, if they are taken seriously at all, have strong objections raised against them. It is one of the obligations of their authors to give serious consideration to these objections and to answer them if possible, since if they fail to do so, it may erroneously be assumed that the theory has been disproved. If the objections cannot be answered in a logical and plausible way with the facts at hand, then either the theory is weak and requires modification or more evidence is needed. In either case, the free exchange of opinions, although seldom completely objective on either side, can serve a useful purpose. Controversy — up to a point — can sometimes be as useful as research in clarifying a problem.

General Considerations

Most of the objections to our tripartite theory of the origin of maize are directed specifically at one of its three parts, but some are of a more general nature. These are

considered here: Weatherwax (30) says of the theory: "Its most obvious general weakness is that there is so much theory in proportion to the available facts. It is topheavy with assumptions of such character that if any one of them should be rejected the whole structure would fall." And in essentially the same words he reiterates (31): "Our principal criticism of this ingenious explanation is that it involves too much theory for the facts. It is top-heavy with premises so interdependent that the failure of any one of them will cause the whole structure to fall."

Whether or not the theory is top-heavy with unsupported premises is largely a matter of personal opinion, and each reader is entitled to his own. However, if Weatherwax's statements were once true, they are certainly less so today, for the theory now has much more evidence in its support than when it was first proposed or even when the objections quoted above were made. Furthermore, these objections have overlooked some of the significant evidence which was even then available. We are disturbed by the fact that the extensive bibliography, which is a part of the joint chapter by Weatherwax and Randolph in a recent book (25), omits a number of significant papers. The omissions are especially unfortunate when the authors cite one paper (26) which they believe supports their conclusions and omit two others published in the same journal (21, 33) which are contrary to them.

The statements with regard to the interdependence of our premises and the charge that "if one of them should be rejected, the whole structure would fall" are simply without foundation. It should be obvious, and in an earlier publication (18) we have emphasized the fact, that the three parts of this theory, although providing an integrated picture of the origin of corn, are, to a large ex-

tent, independent of each other. This becomes clear if we invert the argument and ask whether proof of one part of the theory proves the other two as well. For example, would the discovery of a wild or fossil form of pod corn, although clearly proving pod corn to be the ancestral form, either prove or disprove the assumption that teosinte is a hybrid of maize and Tripsacum or that modern varieties of maize have been modified by introgression from teosinte? Or would proof that teosinte can be artificially produced by hybridizing maize and Tripsacum prove also that pod corn is the ancestral form and that modern corn is strongly contaminated with teosinte?

Since the three parts of the theory are obviously to a large extent independent, it seems appropriate to discuss objections to them separately. The remainder of this paper is concerned only with the first part: the postulate that cultivated corn originated from a form of pod corn. The succeeding papers in this series will treat other aspects of the problem.

Pod Corn, the Ancestral Form

The theory that cultivated maize originated from pod corn, a form in which the individual kernels are enclosed in floral bracts as they are in other cereals and in the majority of grasses, is not original with us, although we have made a contribution to it by adding the assumption that the ancestral pod corn was necessarily quite different from the monstrous pod corn found in modern, highly domesticated varieties. The original idea we owe to Saint-Hilaire (23), who was apparently the first to offer any comment on the origin of cultivated maize and also the first to suggest that pod corn represents the ancestral form. We adopted the pod-corn theory only after our extensive studies of maize-teosinte hybrids had suggested to us that teosinte is itself a hybrid of maize and

Tripsacum and could therefore be dismissed as the ancestor of corn. Pod corn, then, appeared to be the only plausible alternative to teosinte as the progenitor, unless we resorted, as have several of our critics, to a strictly hypothetical ancestral form which is now extinct.

The strongest objections to the pod-corn theory have come from Weatherwax (29, 30, 31). They fall into seven principal categories: (A) Pod corn is "equivocal," a word of many meanings, which when used in this particular context, seems to be more or less synonymous with "extremely variable." (B) It is monstrous and sterile. (C) It is similar to other monstrosities like teopod and corn grass. (D) It does not have the characteristics of a wild grass. (E) It could not have existed in the wild. (F) It is the product of plant hormone action. (G) The weaker form of pod corn, "half tunicate," which at first glance seems to be a more promising ancestral form, affects only the glumes and does not influence the other characteristics of the plant. Let us examine these objections separately.

(A). The first objection is fallacious in two respects: (a) The character, although often variable, is little, if any, more so than other characteristics of the corn plant, such as monoecism and the ear itself—two features which distinguish corn from all other important cereals. If, in attempting to reconstruct the ancestral form, we are to rule out all characters of the corn plant which are highly variable, we can do little more than say that it was a grass, a fact on which all students of the subject have so far been in remarkable agreement. (b) Pod corn actually is not at all equivocal when the genetic background and environment are held constant. Through repeated backcrossing, we have transferred both the *Tu* and the tu^h genes to two inbred strains, A158 and P39. Although the different genotypes which can be produced with the

three alleles at this locus are very different in the two inbreds and their hybrids, there is little if any more variation within the genotype than there is in nontunicate ears of these same inbred strains. The uniformity within any one genotype, when the alleles at the pod-corn locus are incorporated into a uniform genetic background, proves that the variability of pod corn — what has been called its "equivocal" nature — is primarily a matter of variation in the genetic background. What we see in any ear or plant of pod corn is the product not only of the *Tu* or tu^h gene but of these genes interacting with all other genes.

(B). The interaction of the tunicate gene with other genes is an important fact to be remembered in considering the second objection, that pod corn is monstrous. This objection is not only beside the point, since we have always assumed that the ancestor of corn was necessarily a non-monstrous form of pod corn, but it is also not valid. It is, of course, true that modern pod corn is often monstrous, especially when homozygous. We believe, however, that its monstrousness has been misunderstood; pod corn is monstrous today only because it is a wild relict character (a conclusion reached also by Brieger, 4, 5, 6, 7) superimposed upon modern, highly heterozygous and vigorous varieties, some of them the product of teosinte introgression. Today's pod corn is comparable to a 1900 chassis powered by the engine of a 1959 car. The surprising thing is not that pod corn is somewhat monstrous but that it is not more so — that the particular genic locus that governs its expression is capable of functioning at all in a milieu so different from that in which it once served and to which it was undoubtedly well adapted. We have assumed that pod corn would be less monstrous and would exhibit normal grass characteristics when combined with the other "wild" genes. Brieger

(5, 6) sought these in corn's relative, teosinte; we hoped to find them in varieties of popcorn. This hope has been realized as will become apparent later in this paper, when the genetic reconstruction of the ancestral form of corn is described.

The sterility of homozygous pod corn, like its generally monstrous nature, has evidently also been misunderstood. Weatherwax mentions its "self-sterility" — an inaccurate term — and states that little, if any, pollen is produced and that this is rarely functional. Brieger (5) states that the sterility is "still unexplained." Actually, sterility is not an inherent characteristic of pod corn; it is, in fact, nothing more than a strictly physiological or mechanical effect of overgrown glumes. If the glumes are monstrous, the anthers do not reach full development; apparently they do not compete successfully for energy with the rampantly-growing glumes. A potentially sterile tassel of homozygous pod corn can sometimes be induced to become fertile by the early removal of the central spike which is usually massive and bears the most monstrous glumes.

If the glumes are well developed but not particularly monstrous, the anthers may develop normally but fail to be exserted. Under these conditions, they may shed their pollen while still enclosed within the glumes. This pollen, which sifts out between the glumes in considerable amounts, is perfectly normal in appearance and is quite functional. We have produced a number of progenies in which all of the plants were of the genotype *Tutu* by collecting such pollen and applying it to the silks of normal plants.

If the glumes are shortened still further by combining the *Tu* gene with appropriate modifiers, then the anthers not only develop normally but are also normally exserted. We now have strains of homozygous pod corn which

regularly exsert their anthers and shed pollen abundantly. There is no basis whatever for the suggestion (31) that we have, through selection, imparted fertility to a type of maize which never before possessed it. What we have done is merely to reduce the monstrosity of pod corn by combining the *Tu* gene with modifying and inhibiting genes, so that the glumes of the staminate spikelets no longer interfere with the development or release of the pollen. There is no type of pod corn so monstrous or so sterile that it cannot be changed in a few generations to a normal, fertile type by introducing modifying and inhibiting genes from varieties of popcorn.

(C). The comparison of pod corn to other single-gene anomalies in maize, especially teopod and corn grass, is not as significant as it might at first glance appear. It is true that both of these types exhibit certain characteristics which might be regarded as primitive (28, 24): for example, a freely-branching growth habit and seeds partly or completely enclosed by floral structures. And pod corn does indeed resemble teopod and corn grass in being often monstrous. But pod corn, however equivocal and however monstrous, consistently and invariably has one important characteristic which the majority of cereals have and which wild maize is generally assumed to have had: glumes enclosing the caryopses. Both teopod and corn grass occasionally have long glumes; more frequently, perhaps, they bear long spathes (9, 28). Neither of them consistently has the essential wild characteristic of glume-enclosed seeds as does pod corn.

In an earlier publication (13), it was emphasized that a mutation to pod corn has never been observed in pedigreed cultures, which, in the production of hybrid seed corn, involve large numbers of artificially pollinated plants. Weatherwax has contended that the failure to find mutations to pod corn in pedigreed stock "need not

be the cause of much concern" (30), since the occurrence of teopod and corn grass is also infrequent. He is in error. The teopod character has appeared repeatedly in commercial hybrids and is recognized in the hybrid seed-corn industry as a recurring mutant. Corn grass has been found at least twice, according to published reports, and probably many additional times. We know that one corn grass mutant was lost by being hoed out by laborers who thought it to be a weed. How often this has occurred there is no way of telling. In contrast, the mutation to pod corn has never been reported under circumstances where contamination could be ruled out. Millions of ears of inbred strains and their first-generation hybrids have now been studied by corn breeders, and no one has yet reported finding pod corn in a single one.

(D). The contention that pod corn does not have the characteristics expected in a wild grass, especially a freely-branching habit, again overlooks the fact that modern pod corn is the product of a single gene superimposed upon highly domesticated varieties most of which are not themselves freely branching. Weatherwax, himself (27), pointed out many years ago that pod corn is not a variety distinct from all others—that pod corn can be classified as a flint, flour, dent, sweet, or popcorn. By the same token, pod corn can become freely branching if the pod-corn gene is combined with the genes of a freely-branching form. This is well illustrated when pod corn is combined with freely-tillering varieties of popcorn (15). It is strikingly illustrated when it is combined with teosinte, an extremely freely-branching plant.

(E). The assertion that pod corn could not have existed in the wild is based, we believe, on the conception of pod corn as a monstrosity. Certainly the pod corn resulting from incorporating the *Tu* gene in most varieties of modern corn is not promising as a wild plant. However, some

of the strains developed by combining pod corn with popcorn, especially those with tassel seeds, should be quite capable of perpetuating themselves in the wild in a suitable environment.

(F). The suggestion (30) that the characteristics of pod corn are the product of plant hormone action is quite valid but wholly irrelevant. It is undoubtedly true that pod corn involves plant hormone action, but we do not see how this fact can be regarded as evidence against the idea of pod corn as the ancestral form. We would assume that some of the principal changes which have occurred in the maize plant during the course of its evolution under domestication are concerned with the nature and amount of various plant hormones or in the manner in which these act. Indeed, we suspect that one of the effects of the pod-corn gene is to direct the plant's energy into terminal inflorescences and that one of the reasons why modern homozygous pod corn is usually monstrous is because all of the energy of a massive single stalk goes into a single terminal inflorescence. Our crosses of pod corn and popcorn indicate that terminal inflorescences are less monstrous when they occur on a plant with a number of stalks. A freely-tillering plant undoubtedly has a different hormonal complex than a single-stalked one.

(G). The conclusion that the half-tunicate form of pod corn, although in some respects more promising as a wild ancestor than the full tunicate, involves only the glumes of the ear, is erroneous and results from confusing half tunicate with the character, first recognized as "pallee sviluppate" by Bonvicini (3), later by Andres (2) as "semivestidos" and more recently by Galinat (10) as "papyrescent." Weatherwax's (30) illustration of half tunicate is almost certainly that of a papyrescent ear. Mangelsdorf (13) once made a similar error but was fortunate, as the result of test crosses, in discovering it be-

fore drawing conclusions about the nature of pod corn. The ear of Peruvian corn, which he illustrated (13) as a form of pod corn, proved upon further study, including its introduction into uniform inbred strains, to be not half tunicate but rather the character now known as papyrescent. This character does appear to affect only the glumes of the pistillate inflorescence and in this respect differs decidedly from half tunicate which, as will be shown by data presented later, produces virtually all of the effects of tunicate, only in a lesser degree.

We ourselves have given serious consideration to the possibility that half tunicate, rather than tunicate, is the ancestral type and that the latter may be an extreme form — the product of a pseudoallelic locus which has arisen during domestication as a mutation resulting from the duplication of an existing locus. We do not yet rule out this possibility; indeed we have for some years been developing stocks to determine whether the *Tu* locus is a compound one whose elements are sometimes separated by crossing over to produce "mutations" to half tunicate.

A preliminary experiment on this point conducted in the summer of 1958 produced one apparent mutation from tunicate to half tunicate which was accompanied by crossing over between the *su* and *gl*$_3$ loci on chromosome 4.

But whether tunicate or half tunicate is the ancestral form is of secondary importance since both are pod corn and both involve the *Tu* locus on chromosome 4. There can be no doubt that there have been changes at this locus and little doubt that these changes have been a factor in corn's evolution under domestication. This is demonstrated by the facts set forth below.

The Effects of the Alleles at the *Tu* Locus

One result of our intensive study of pod corn has been

the discovery of alleles, previously unknown, at the *Tu* locus, the most useful of which is the intermediate allele tu^h. By incorporating the two higher alleles in the series, *Tu* and tu^h, into a uniform inbred strain (A158) through repeated backcrossing, it has been possible to produce six distinct genotypes as follows: *TuTu*, *Tutu*^{h}, *Tutu*, tu^htu^h, tu^htu, *tutu*. A comparison in a large number of characteristics of these six genotypes has now been made and the data have been briefly summarized in a preliminary statement (16) and will be reported in detail elsewhere. It can be said here that a comparison of the six genotypes, which are isogenic except for the *Tu-tu* locus, provides a clearer understanding than we have had before of what these genes actually do. And what they do is both remarkable and highly significant with respect to gaining a conception of corn's evolution under domestication. Data on several of the characteristics which were studied are presented in TABLE I. They show that in proceeding through this series of six genotypes in the direction from *TuTu* to *tutu* the following changes occur: (a) A decline in the prominence of the terminal inflorescence, the tassel, and a corresponding increase in the development of the lateral inflorescence, the ear. (b) A change from a predominantly pistillate tassel to a wholly staminate one. (c) A progressive decrease in the length and weight of the glumes and a corresponding increase in the size and weight of the rachis.

All of these profound changes are of a kind which might have occurred in evolution under domestication; all of them tend to make the corn plant less able to survive in the wild and more useful to man. It is important to note, for example, that reduction in the weight of the tassel has been accompanied by an increase approximately five times as great in the weight of the ear, the food-storage organ. Likewise, the reduction in the pistillate

TABLE I. Six isogenic stocks, differing in alleles at the *Tu* locus, compared in various characteristics.

Characteristics	Genotypes					
	TuTu	*Tutu^h*	*Tutu*	*tu^{h}tu^h*	*tu^{h}tu*	*tutu*
Total weight inflorescences, gms.	28.9	39.9	72.2	98.9	133.3	130.1
Weight of tassels	28.9	18.3	12.7	9.2	6.7	4.9
Weight of ears	0.0	21.6	59.5	89.7	126.6	125.2
Percentage of total in ears	0.0	54.1	82.4	90.7	95.0	96.2
Percent pistillate spikelets in tassels	79.9	0.9	0.0	0.0	0.0	0.0
Average length staminate glumes, cms.	2.7	1.9	1.7	1.4	1.2	1.0
Total weight of cobs, gms.	0.0	6.4	20.6	24.5	24.0	22.7
Weight of pistillate glumes	0.0	5.3	16.5	17.7	14.2	8.7
Weight of rachises	0.0	1.1	4.1	6.8	10.5	10.9
Percentage of total in rachises	—	17.2	19.9	27.8	42.5	55.6

glumes, which are not needed in cultivated maize, has been accompanied by an increase in the size and weight of the rachis, which is both the grain-bearing structure and the container of the system of supply. In short, a substantial part of corn's evolution under domestication can be explained by a change in the hereditary material at this single locus. No such profound and significant changes in the direction away from a wild plant toward a highly useful, domesticated one can be demonstrated for teopod or corn grass or any other character in corn.

Perhaps it should be stated that we do not regard the monstrous pod corn represented by the genotype *TuTu* in this particular series as a model of the ancestral form. It probably does have some of the essential characteristics of wild corn—tassel seeds, long glumes, slender rachises —but in highly exaggerated forms. Consequently a comparison of the six genotypes on this particular genetic background provides a kind of biologically magnified view of some of the changes which have occurred in evolution under domestication.

The Evidence from Prehistoric Corn

If pod corn is the ancestral type, it should occur in some collections of prehistoric corn and possibly in representations on prehistoric pottery. It was while searching for such representations that we discovered in the Peabody Museum of Yale University a ceramic specimen which we described some years ago as possibly being pod corn (17). We also illustrated a second specimen from the same museum which might be so interpreted. Since then, we have seen ceramic replicas which might represent pod corn in the Museum of the University of Pennsylvania and in the Museum of the University of Cuzco in Peru. Two of the latter are illustrated by Weatherwax (30, Fig. 44).

Weatherwax (30) doubts that the Peabody Museum specimens represent pod corn and suggests that they are replicas or even casts[3] made from nontunicate ears whose overlapping grains have long, attenuated tips. He illustrates such an ear (30) and suggests that it might have served as a model for the prehistoric ceramic specimens.

Weatherwax has overlooked an important difference between one of the ceramic replicas and the modern Peruvian ear with imbricated kernels—the variation in length of the individual units. The glumes of pod corn are usually longest at the base of the ear and become progressively shorter toward the tip. This is well illustrated in Weatherwax's Fig. 51 (lower center) which shows variation in the spikelets of a single ear of pod corn. This same kind of variation is exhibited in some degree in the units of the prehistoric ceramic replica but it is conspicuously absent in the kernels of the modern Peruvian ear (cf. Weatherwax, Fig. 51, upper left, center and right).

[3] There is no possibility of making a realistic representation of overlapping kernels from the cast of an ear; each kernel must be fashioned separately and inserted in its proper place.

Consequently our original interpretation of the ceramic specimen as possibly representing pod corn still seems to us more plausible than Weatherwax's.

Weatherwax's suggestion is, however, quite useful in raising an entirely different question. Why are non-tunicate ears with pointed, imbricated kernels common in Peru and other countries of Latin America (6, 22, 32, 34) and why are they even more common in archaeological specimens and in prehistoric ceramic replicas (17, 30, 35, 36)?

One answer to this question—the correct one we suspect—is that pointed, imbricated kernels represent, as does pod corn, an ancient, relict, wild character which still persists in cultivated corn especially in certain Peruvian races. We know that kernels of modern pod corn are often pointed; they are squeezed into this shape during their development by the pressure of glumes. Indeed, when occurring in the tassels, if they fail to become pointed through pressure, they spread the glumes apart thus inviting the depredations of insects and birds. Such a characteristic would have a low survival value in nature. Consequently, we are forced to assume that, although the kernels of wild pod corn were pointed, this shape was determined in part genetically and not alone by pressure applied during development, as is also the case in the kernels of corn's relatives, Tripsacum and teosinte. When the tunicate character was lost through mutation the pointed, imbricated grains persisted for a time and are still found widely distributed in some varieties. They are, however, less common now than they were prehistorically and are probably destined to disappear completely, since they have no apparent survival value.

Here is an excellent example of the usefulness of controversy. By raising doubts about our conclusions on the

nature of prehistoric replicas of pod corn, Weatherwax has compelled us to examine the significance of pointed, imbricated kernels with the result that we have found a far more plausible explanation for their occurrence than that which we had earlier (17) proposed—the introgression of Tripsacum and teosinte.

More useful than ceramic replicas are actual prehistoric specimens. Mangelsdorf (13) pointed out that many prehistoric cobs have the deep pockets, with the general aspects of a honey comb, of heterozygous half tunicate and concluded that these represent a weak form of pod corn. Later, Mangelsdorf and Smith (19) found that many of the prehistoric cobs of Bat Cave have the long glumes and slender rachises characteristic of weak pod corn and concluded that these, like the Peruvian cobs, involve an expression of alleles at the *Tu* locus. Both Weatherwax (29) and Randolph (20) have expressed skepticism of the conclusion. Weatherwax's statement on this point follows:

> The illustrations shown are not very convincing as to the tunicate character of the materials at any level, and there must be something wrong with the artist's reconstruction of the primitive podded ear, in which the *individual grains*, rather than the *pairs of grains*, seem to be spirally arranged.

The suspicion that " . . . there must be something wrong with the artist's reconstruction . . . " is a classic example of an observation colored by inhospitality to an unwelcome idea. The fact is that the artist's reconstruction was printed side by side with an actual photograph of the prehistoric specimen which shows clearly that the individual spikelets are indeed spirally arranged. Nor is this an unusual pattern in prehistoric corn. It would be surprising if Weatherwax had not himself encountered it. Anderson (1) described some of the prehistoric Peruvian specimens as having cross spirals, like a pine cone.

It is unfortunate, we think, that Weatherwax's erroneous statement, which reflects upon the accuracy of the artist, has never been corrected, although there have been several opportunities in subsequent publications for doing so.

The basis for skepticism regarding the tunicate nature of other prehistoric specimens which we have described as weak forms of pod corn is little if any better. It is true that only a few prehistoric specimens resembling modern pod corn have been found (8, 11), but this is not, in any case, the kind of pod corn that we should expect to find commonly among prehistoric specimens. If modern pod corn is monstrous because it has lost its modifiers, then prehistoric pod corn, not so far removed from wild corn, should be a more restrained form. As mentioned above, Mangelsdorf (13) has shown that some of the prehistoric corn of Peru has glumes similar to those occurring in heterozygous, half-tunicate modern maize. More recently, we have discovered (15) in a variety of popcorn a major inhibitor of the tunicate character and it has been possible by combining this gene with the *Tu* and tu^h genes to synthesize a wide range of types matching many of the prehistoric specimens. We know of no other way in which such matching specimens can be synthesized.

The question of whether or not the prehistoric corn with relatively long glumes and slender rachises is pod corn finally becomes little more than an exercise in semantics. Randolph, for example, states (20):

> It is difficult to see in these specimens of the most ancient cultivated maize thus far discovered, or in the existing wild relatives of maize, any support for the hypothesis that maize originated from a primitive type of pod corn of the sort that is known to be controlled by the dominant *Tu* allele in chromosome 4 of maize.

And Weatherwax, in commenting upon the possible

differences between modern cultivated corn and the original pod corn, states (30):

> It may be contended that these deficiencies of pod corn are due to characteristics of cultivated corn which have been superimposed upon its original nature by recent hybridization, but there is a question as to how much liberty of this sort we may take with the plant and still call it pod corn or talk about its characteristics as being primitive.

It is true that when we proposed the pod-corn theory we had in mind a restrained form of pod corn controlled by the *Tu* gene on chromosome 4 in combination with a complex of modifying factors. Since then, as the result of intensive studies of pod corn, stimulated and guided by this part of our theory, we have discovered not only lower alleles at this locus but also modifying and inhibiting factors. Various combinations of these alleles and modifying and inhibiting factors can produce a gamut of types ranging from those in which the glumes are scarcely longer than those of modern varieties of sweet corn to those in which the glumes are several inches in length. In this wide range, where does normal corn end and pod corn begin? We have weak forms of the genotype *Tutu* whose glumes are much less conspicuous than those found in monstrous forms of the genotype $tu^h tu^h$. Is one of these pod corn and the other not and which is the pod corn?

Until specimens matching prehistoric cobs are synthesized by methods other than the one which we have successfully employed—that of combining alleles at the *Tu* locus with inhibiting and modifying factors—we shall continue to assume that these prehistoric specimens possessing relatively long glumes and slender rachises are forms of pod corn.

Pod Corn in Living Varieties

The conclusion that changes at the *Tu* locus on chromosome 4 represent an important factor in the evolution

of maize under domestication is further supported by the occurrence—more widespread than had previously been suspected—of various forms of pod corn among the living varieties of this hemisphere. The extreme form conditioned by the *Tu* gene has been found in Colombia, Brazil, Peru and Bolivia. It is apparently quite common in Bolivia where, according to a report from Señor Dick Edgar Ibarra Grasso, Director, Museo Arqueológico, Universidad Mayor de San Simon, Cochabamba, Bolivia, it occurs in many of the valleys on the eastern slopes of the Andes.

The half-tunicate form of pod corn controlled by the tu^h locus has appeared in varieties from Ecuador, Paraguay and Peru (14). It, or something like it, is rather common in a Peruvian coastal race, Perla. Mr. Alexander Grobman of the National School of Agriculture near Lima has reported that one to two percent of the inbred strains isolated from this race are segregating for half-tunicate; in some collections the frequency is even higher.

How is this situation to be explained? Either wild corn was pod corn and had the genotype *TuTu* or tu^htu^h or it was not and had the genotype *tutu*. If it was not pod corn, then the *Tu* and tu^h genes now found in corn must represent mutations from the lower allele to the higher alleles in the series. Mutations from lower to higher alleles do occur but are not common. More difficult to explain is the preservation of these higher alleles if they are not the original ones. We can perhaps imagine that the pod corn controlled by the *Tu* allele was preserved by man as a curiosity or for its supposed magical properties, but this could scarcely be true of the weak pod corn controlled by the tu^h gene since in the heterozygous condition it is not generally recognized. Yet, because of competition between glumes and kernels, the weak pod corn undoubtedly causes some reduction in the yield of grain

and would be expected to have a low survival value. Why, then, should this allele have even a higher frequency than the *Tu* allele?

All of these difficulties can be avoided and the problem becomes quite simple if we assume instead that wild corn was *TuTu* which gave rise through mutations to the lower alleles, tu^h and *tu*. The *Tu* gene has largely disappeared; the tu^h gene is in the process of disappearing; and it would seem that eventually all of the world's corn will be *tutu*, the most efficient genotype from the standpoint of usefulness to man.

Another assumption mentioned earlier, which is almost equally simple and plausible, is that wild corn was half tunicate, $tu^h tu^h$, which, through mutation, gave rise to the nontunicate genotype, *tutu*, and, through unequal crossing over, to the strongly tunicate form *TuTu*. The first might have been preserved because of its obvious usefulness, the second because of its supposed magical properties.

It should be noted that both of the above assumptions postulate that the progenitor of cultivated corn was a form of pod corn and that changes at the *Tu-tu* locus have been involved in corn's evolution under domestication.

Reconstructing the Ancestor of Corn

Perhaps the strongest support for the pod-corn theory is provided by a genetic reconstruction of the ancestral form (15). This was accomplished by crossing pod corn with a number of freely-tillering varieties of popcorn and through selection combining the *Tu* gene with a complex of minus modifying factors and a majoring inhibiting factor. The plants so produced have several stalks; the tassels bear both male and female flowers, the former above and the latter below on the same branches; the

branches are brittle when mature, breaking apart easily when disturbed by the wind or by birds, thus providing a mechanism for the dispersal of the seeds. When ears occur, they are borne at high positions on the stalk. In these positions, the ears are small, sometimes branched, bear both male and female flowers, and are enclosed by only a few husks which flare open at maturity, allowing the fragile ear to disperse its glume-covered seeds. Plants of this reconstructed ancestral form have many of the characteristics of a good wild grass, and they show a striking similarity in several of their botanical characteristics to Tripsacum, a wild relative of maize. As mentioned above, this reconstructed form, with some additional modifications brought about by selection, might survive in nature in a suitable environment.

This true-breeding pod corn shows a resemblance in its principal botanical characteristics to Weatherwax's hypothetical ancestor of the American Maydeae which he described as follows (29):

> We picture the ancestral form as a plant with the habit of teosinte or of some of the tropical species of *Tripsacum*, with paniculate inflorescence terminating the main culm and the branches. Each inflorescence had pairs of staminate spikelets in the terminal portion and pairs of pistillate spikelets toward the base of each of its branches. The staminate spikelet was two-flowered, but the pistillate had only one functional flower and a rudiment of another. The lower glume of the pistillate spikelet and the adjacent rachis segment had probably not yet developed into a hard shell.

Except that it is an annual and often has both male and female spikelets in both inflorescences, the reconstructed form is similar to the hypothetical wild maize with which domestication began, described by Weatherwax as follows (29):

> It is conceivable, however, that there came a time when, by natural processes, it had taken on an appearance not very different from that of some relatively undeveloped varieties cultivated today. That is, it had terminal staminate panicles on a few main culms and pistillate

panicles in various stages of reduction to the spicate form on numerous branches. The small ears, with eight or more rows of grain, were partly enclosed in the leaf sheaths, and the small grains were partly enclosed in the bracts of the spikelets.

How are we to account for the close resemblance between Weatherwax's hypothetical and our genetically reconstructed ancestral form? Weatherwax has assumed that the nature of corn's progenitor could be deduced from a study of the characteristics of its living descendants and relatives. We have assumed that genes controlling the principal characteristics of wild corn are not likely to have been completely lost in several thousand generations of domestication; that they still exist in cultivated varieties; and that the ancestral form can be reconstructed by recombining them. The fact that the two methods produce essentially the same end result is either a remarkable coincidence or an indication that both methods are valid and that the picture of corn's ancestor which both produce may be a reasonably accurate one.

Summary

The evidence for and against the pod-corn theory has been reviewed; the principal objections to it have been considered; and plausible answers to all of them have been found in the evidence now at hand.

1. Pod corn is "equivocal" only when its genetic background is variable. In inbred strains or in uniform F_1 hybrids the pod character is no more variable than other characteristics of the plant.

2. Modern pod corn is often monstrous and sometimes sterile because it is the product of an ancient relict gene superimposed upon highly heterozygous, vigorous modern varieties. It is neither monstrous nor sterile when combined with other primitive characters.

3. Pod corn differs from other monstrous forms such as teopod and corn grass in always exhibiting one characteristic which wild corn must have had: kernels enclosed and protected by glumes.

4. When pod corn is combined with some of the genes of certain varieties of popcorn it exhibits a number of characters of a wild grass: a freely-branching growth habit, small pointed seeds, glumes enclosing the seeds and a means of seed dispersal.

5. The fact that pod corn may be the product of plant hormone action does not rule it out as the ancestral form. Changes in plant hormone systems are to be expected during evolution under domestication.

6. Although modern monstrous pod corn could not exist in the wild, some of the forms produced by crossing popcorn and pod corn are probably capable of doing so in a suitable environment.

7. The conclusion that the half-tunicate form of pod corn could not be the ancestral type because it involves only the glumes is a result of confusing this characteristic with another, the papyrescent.

8. The fact that pointed, imbricated kernels have a higher frequency in prehistoric corn than in modern corn suggests that they represent a primitive character once associated with the podded condition.

9. Prehistoric cobs suspected of representing various types of pod corn can be matched by combining the alleles of the *Tu* locus with various modifying and inhibiting genes.

10. One of the lower alleles of pod corn, tu^h, has a high frequency in living varieties. This would not be expected if wild corn had been of the genotype *tutu* and if tu^h represents a mutation occurring during domestication.

11. A genetically reconstructed ancestral form produced by combining the characteristics of pod corn with those of certain varieties of popcorn is identical in virtually all of its characteristics with the hypothetical ancestral form, based upon comparative morphology, described by Weatherwax.

12. It is concluded that the pod-corn theory now has greater validity and more evidence in its support than when it was first proposed.

LITERATURE CITED

1. Anderson, E., 1947. Corn before Columbus. Pioneer Hi-Bred Corn Co. Des Moines.

2. Andres, J. M., 1950. Granos semivestidos, restos de un carácter ancestral del maiz. Revista Argentina Agron. 17: 252–256.

3. Bonvicini, M., 1932. Sulla eraditarietà di una anomalia nel mais. L'Italia Agricola 69: 3–9.

4. Brieger, F. G., 1943. Origem do milho. Revista de Agric. 18: 409–418.

5. ——, 1944. Estudos experimentais sôbre a origem do milho. Anais Escola Superior Agric. "Luiz de Queiroz" Seperata No. 10: 226–278.

6. ——, 1945. Estudos genéticos sôbre o milho tunicata. Anais Escola Superior Agric. "Luiz de Queiroz" Seperata No. 17: 209–238.

7. ——, 1945. Estudos sôbre a inflorescência de milho com referência especial aos problemas filogenéticos. Bragantia 5: 659–716.

8. Cutler, H. C., 1944. Medicine men and the preservation of a relict gene in maize. Jour. Hered. 25: 290–294.

9. Galinat, Walton C., 1954. Corn grass II. Effect of the corn grass gene on the development of the maize inflorescence. Amer. Jour. Bot. 41: 803–806.

10. ——, 1957. The effects of certain genes on the outer pistillate glume of maize. Bot. Mus. Leafl. Harvard Univ. 18: 57–76.

11. ——, P. C. Mangelsdorf and L. Pierson, 1956. Estimates of teosinte introgression in archaeological maize. Bot. Mus. Leafl. Harvard Univ. 17: 101–124.

12. Mangelsdorf, P. C., 1947. The origin and evolution of maize. Advances in Genetics 1: 161–207.

13. ——, 1948. The role of pod corn in the origin and evolution of maize. Ann. Missouri Bot. Gard. 35: 377–406.

14. ——, 1957. Half-tunicate from Peru, Ecuador and Paraguay. Maize Gen. Coöp. News Letter 31: 64.

15. ——, 1958. Reconstructing the ancestor of corn. Proc. Amer. Philos. Soc. 102: 454–463.

16. —— and Helen P., 1957. Genotypes involving the *Tu-tu* locus compared in isogenic stocks. Maize Gen. Coöp. News Letter 31: 65–66.

17. —— and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exp. Sta. Bull. 574.

18. —— and R. G. Reeves, 1945. The origin of maize: present status of the problem. Amer. Anthropologist 47: 235–243.

19. —— and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harvard Univ. 13: 213–247.

20. Randolph, L. F., 1952. New evidence on the origin of maize. Amer. Nat. 86: 193–202.

21. Reeves, R. G., 1950. The use of teosinte in the improvement of corn inbreds. Agron. Jour. 42: 248–251.

22. Roberts, L. M., U. J. Grant, R. Ramirez E., W. H. Hatheway and D. L. Smith, *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize of Colombia. Nat. Acad. Sci.—Nat. Res. Council Publ. No. 510.

23. Saint-Hilaire, A. de, 1829. Lettre sur une variété remarquable de maïs du Brésil. Ann. Sci. Nat. 16: 143-145.

24. Singleton, W. R., 1951. Inheritance of corn grass a macromutation in maize, and its possible significance as an ancestral type. Amer. Nat. 85: 81–96.

25. Sprague, G. F., 1955. Corn and corn improvement. New York, Academic Press.

26. Vachhani, M. V., 1950. A study of the relationship of chromosome knobs with certain agronomic and morphological characters in corn inbreds. Agron. Jour. 42: 196–201.

27. Weatherwax, P., 1923. The story of the maize plant. Univ. Chicago Press.

28. ——, 1929. The morphological nature of teopod corn. Jour. Hered. 20: 325–330.

29. ——, 1950. The history of corn. Sci. Month. 71: 50–60.

30. ——, 1954. Indian corn in old America. New York, Macmillan.

31. ——, 1955. History and origin of corn I. Early history of corn and theories as to its origin. *In* Corn and corn improvement: 1–16. New York, Academic Press.

32. Wellhausen, E. J., A. Fuentes O. and A. Hernandez C., *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize in Central America. Nat. Acad. Sci.–Nat. Res. Council Publ. No. 511.

33. —— and C. Prywer, 1954. Relationship between chromosome knob number and yield in corn. Agron. Jour. 46: 507–511.

34. ——, L. M. Roberts and E. Hernandez X., *in collaboration with* P. C. Mangelsdorf, 1952. Races of maize in Mexico. Bussey Inst. Harvard Univ.

35. Wittmack, L., 1880. Ueber antiken Mais aus Nord-und Südamerika. Zeitschrift f. Ethnologie 12: 85–97.

36. ——. Plants and fruits. *In* Reiss and Stübel, The Necropolis of Ancon in Peru. Vol. III, Part XIII. London and Berlin. 1880–1887.

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THE ORIGIN OF CORN
II. TEOSINTE, A HYBRID OF CORN AND TRIPSACUM

BY

ROBERT G. REEVES AND PAUL C. MANGELSDORF

THE tripartite theory of the origin of corn (26) holds, among other things, that teosinte (*Zea mexicana*) originated as a hybrid between corn and Tripsacum, which backcrossed to corn one or more times. In 1939, the hybridization was postulated as having occurred well after corn had been domesticated, perhaps as late as 900 A.D. Reeves, however, later (35) favored the suggestion of Stebbins (47) that it might have occurred much earlier, possibly at a time when corn and Tripsacum possessed somewhat the same plant characters as now but when they were more interfertile. Mangelsdorf and Smith (28) reported archaeological evidence that teosinte came into existence not later than 500 B.C. and perhaps earlier.

Both Weatherwax (51, 52, 53) and Randolph (31, 32) raised objections to this part of the theory, objections which fall into the following categories: (A) A cross as difficult to make as that of corn and Tripsacum could not have occurred in nature. (B) Tripsacum chromosomes and genes have a negligible effect when in combination with corn germplasm. (C) The frequency of interchange or crossing over between corn and Tripsacum is not sufficient to give rise to a new intermediate species by intro-

gression. (D) The apparent relationship of chromosome-knob numbers with geographical distribution is a fallacy or is not pertinent to the problem. (E) The chromosomal characters of corn, teosinte, and Tripsacum are not consistent with the theory that teosinte originated as a hybrid between corn and Tripsacum. (F) There is no cytological mechanism by which the terminal knobs of Tripsacum could have assumed the internal positions now found in some varieties of teosinte. (G) The fact that teosinte is intermediate between corn and Tripsacum in plant characters is of minor importance.

These objections will be considered in the order named, with emphasis on recent results obtained by various investigators; for completeness two additional topics will be discussed.

Possibility of Natural Hybridization of Corn and Tripsacum

The first crosses of corn by Tripsacum, on which our earlier studies were based, were made only after removing the shucks of corn and pruning the silks. But we have found since 1939, as Randolph also has, that the pruning of the silks, although probably helpful, is not essential to hybridization.

Since they appear to have been overlooked, we shall repeat two possibilities previously mentioned (26) by which corn might become hybridized naturally with Tripsacum: (a) the occurrence of ears which protrude beyond the shucks, a common character in certain varieties; (b) silks exposed to the base through mutilation of the shucks by insects or by holes bored by larvae.

Weatherwax's own publications (51, 52, 53) mention or describe at least four additional conditions in corn—depauperate plants with terminal pistillate inflorescences, homozygous pod corn, flowering tillers and his hypo-

thetical ancestor of modern corn—in which the silks are exposed to pollen for their entire length. Also from Weatherwax's laboratory has come what is perhaps the most significant evidence on this point. Farquharson (14) demonstrated that certain varieties of Tripsacum, when used as female parents, crossed readily with corn without the use of special techniques. She states: "In fact, it seems highly probable that this cross has occurred occasionally in nature."

Randolph's objection to this part of our theory is based on his own experiments in crossing Mexican and Guatemalan varieties of corn with Mexican and Guatemalan Tripsacum. Although these experiments may seem to have the virtue of directness, they are far from critical in several respects. The number of ears pollinated, 612, seems impressive at first glance, but a critical analysis suggests that successful crossing on a scale proportional to the numbers involved could hardly have been expected, especially because of the high frequency in these areas of the *Ga* gene which produces cross sterility. These experiments likewise fail to take into account two important facts: (a) that the corn and Tripsacum of today is not the same as was that of ancient times; (b) that even the modern types of corn and Tripsacum of the region have not been completely sampled.

Cutler and Anderson (11), in a survey of the genus Tripsacum, did not find *T. dactyloides* south of the United States–Mexican border. Fourteen years later, Randolph (32) stated twice that *T. dactyloides* has still not been reported south of the Mexican border and that this species therefore could not have been involved in the assumed recent hybridization with corn in Guatemala or neighboring areas. Apparently, he was not aware that Melhus (29) two years earlier had reported the occurrence of this species in Guatemala. Mangelsdorf (unpub-

lished) has identified prehistoric Tripsacum, apparently *T. dactyloides*, from El Diablo Cave, Tamaulipas, Mexico and has found the same form growing in the vicinity. A general appraisal of the evidence published to date suggests that, of all forms tested, a 2n=36 type of *T. dactyloides* is the one most likely to produce a fertile, intermediate, backcross hybrid; this has virtually all the plant characters that would be required. The main objection is that, in combination with corn varieties with which it has been tested, this type falls a little short of being sufficiently interfertile. In 1939, we (26) pointed out several additional characters which, at that time, seemed to make it unsuitable as a putative parent. Although most such characters now have been explained in accordance with the theory of hybrid origin (34), a form of Tripsacum which meets the requirements better than those now known may yet be found in the future.

It seems desirable to consider here the implications of the suggestion made by Anderson (1), and now supported by Farquharson's experimental results (13), that the form of *T. dactyloides* currently regarded as diploid might be in reality an allotetraploid. If the center of origin of Tripsacum is in Mexico or Guatemala, as both Weatherwax and Randolph conclude, it would be natural to suppose that either *T. dactyloides* (2n=36) or its parents once occurred there. In this event, one of the parents (2n=18) of *T. dactyloides* and a primitive corn might be the parents of teosinte (47). However, we do not wish to base the case for the hybrid origin of teosinte on ancestors still unknown or now extinct. Rather we would emphasize that teosinte could be derived through the hybridization of existing forms.

The Effects of Tripsacum Chromosomes and Genes

In our first hybrids between corn and Tripsacum (26),

the only functional gametes of F_1 plants were unreduced, and repeated backcrossing to corn produced progenies which segregated for 2n and 2n+1 classes. The extra chromosome of the 2n+1 plants no doubt was derived originally from Tripsacum, and the two genoms of both classes of plants were originally corn chromosomes. In pachytene and diakinesis of the 2n+1 plants, the extra chromosome synapsed in low frequency with one of the pairs of corn chromosomes, forming a trisome. In other plants where several Tripsacum chromosomes were present, weak synapsis occurred between additional corn and Tripsacum chromosomes. Genetical results showed that an allele of su_1, not completely dominant to su_1 of corn, was transferred from Tripsacum to corn chromosome 4. In vegetative characters, the 2n+1 plants were so different from their 2n sibs that the two classes could usually be distinguished at a glance. The presence of a single Tripsacum chromosome resulted in partial sterility, both male and female.[1]

The work of Maguire (21, 22) confirmed the salient cytogenetical features reviewed above, except that in her stocks one extra Tripsacum chromosome produced only a negligible effect on the corn phenotype and no reduction in ear fertility. In light of the possibility that the forms of Tripsacum with 36 somatic chromosomes might actually be tetraploids, as Farquharson's (13) work strongly indicates, the results obtained by Maguire, and especially an interpretation placed on them by Randolph, are in need of review.

Maguire's cytological material consisted of seven stocks, which she stated were possibly distinct in the

[1] In an earlier publication (26), we attempted to estimate the number of Tripsacum chromosomes present from the degree of pollen sterility. We have since become convinced from Maguire's studies, as well as our own, that this method has little, if any, value.

sense that each stock may have had a different Tripsacum chromosome. She (21) explained that it was impossible to determine how many of the seven were really different. Randolph (32) stated positively that the stocks were trisomic for seven different Tripsacum chromosomes. Maguire's results justify her cautious statement that the seven stocks were "possibly" distinct. She stated repeatedly that her Tripsacum chromosomes number 4 and 5 were very similar to one another and that they resembled B-chromosomes, although the Tripsacum parent had only 36 chromosomes and the corn parent had no B-chromosomes. In addition, her numbers 2, 6 and 9 were similar to each other in size, morphology, behavior and effect on pollen sterility. We venture the opinion that her seven stocks contained no more than four different Tripsacum chromosomes, possibly even fewer. A final conclusion on this question must await better evidence; in the meantime, there is serious doubt that Tripsacum contains seven different chromosomes, all without phenotypic expression in the presence of two corn genoms.

In this connection, a brief review of unpublished experimental results obtained by Reeves on a population of corn-Tripsacum hybrids may be useful. During the season of 1955, 45 hybrid plants of Texas Inbred 203× diploid *Tripsacum dactyloides*, backcrossed three times to Inbred 203, were grown. Cytological examination was made on 17 of them taken at random, and each plant examined contained one extra chromosome, sometimes with additional irregularities. None of the 45 plants dehisced any pollen. When anthers of each plant were dissected for pollen examination, no more than a dubious trace of starch was found in any of the many thousands of grains examined, and about 99 per cent of them were completely empty. The greatest number of seeds produced by any of the 45 plants was 98, and the average

was 28.6, although each plant was pollinated several times with corn pollen.

Data taken on phenotypic characters of these BC_3 plants revealed several significant differences between this population and Inbred 203, the only corn line which had entered the ancestry of the hybrids, but we shall discuss only one of these—number of rows of alicoles. This character is not only one by which the parents of this cross differ, but it is also one of the generic characters distinguishing corn and Tripsacum. With all the plants growing in the same relatively uniform nursery, planted the same day and given the same treatment, Inbred 203 had a mean of 6.48 rows of alicoles and the BC_3 hybrids a mean of 4.38. This difference was highly significant statistically, and the deviation of the hybrids from their corn parent was in the direction of Tripsacum.

During the 1956 season, 290 offspring resulting from the fourth backcross to Inbred 203 were grown, and, except for a few differences which will be pointed out, the results were essentially a repetiton of those obtained in 1955. The mean number of alicole rows for Inbred 203 in 1956 was 6.36 and that for the hybrids 4.15, and again the difference between the means was highly significant. Although 288 plants of this population of 290 were completely pollen sterile and showed no greater ovule fertility than did the third backcross generation, two plants dehisced an abundance of pollen and produced approximately full ears of grains when selfed. The ear of one of these fertile plants had six rows of alicoles and that of the other seven rows, both numbers near the average of Inbred 203. It might be of incidental interest, however, to note that in certain other characters, such as number of tassel branches and height of upper ear node, one plant or the other was not within the observed range of variation of Inbred 203; and the deviation here again

was in the direction of Tripsacum. Work on these hybrids is still in progress, and more data will be needed to explain what is occurring in them. But a tentative conclusion is justified: that all of them up to and including the sixth backcross generation, with rare exceptions, had one extra Tripsacum chromosome and showed phenotypic effects of it.

Interchange Between Corn and Tripsacum Chromosomes

With respect to crossing over between corn and Tripsacum chromosomes, Maguire's (21, 22) observations, confirming our own of 1939, showed clearly that some form of exchange had occurred. Maguire (22) concluded that the end of the long arm of a Tripsacum chromosome and the end of the short arm of corn chromosome 2 are sufficiently homologous to allow apparently normal pairing, and that the terminal knob of the Tripsacum chromosome was occasionally transferred to corn chromosome 2 by some mechanism other than normal crossing over. Our earlier publication (26), which reported a gene exchange in a similar hybrid at the *su*$_1$ locus of corn accompanied by cytological evidence of crossing over, made no claim as to the frequency or the exact nature of such exchanges, and our hypothesis of the hybrid origin of teosinte did not, and still does not, require a decision on these questions. According to this hypothesis, a single successful hybrid between corn and Tripsacum, followed by a few exchanges at such positions in the chromosomes as to replace certain blocks of corn genes with blocks of Tripsacum genes, is all that is required. Yet Randolph (32) continues to be perturbed by the apparent fact that the association between corn and Tripsacum chromosomes is not followed by the "expected frequency" of crossing over.

Babcock (2) found a relationship closely parallel to that between teosinte and its putative parents, corn and Tripsacum, in section *Ixeridopsis* of the genus *Crepis* and drew a similar conclusion. The morphological and cytological evidence indicates that this section is transitional from genus *Crepis* to genus *Ixeris*, but its phylogenetic position hardly permitted its being considered an ancestral group from which *Crepis* and *Ixeris* were derived. The somatic chromosome number of *Ixeris alpicola* and of section *Ixeridopsis* is 14, but no other group within the genus *Crepis* has this number. Babcock considered it plausible that this section resulted from hybridization between *Ixeris* and *Crepis* at a time when the present generic divergencies were not so strongly developed as now. In another section, *Pyrimachos*, the parallel is again similar to teosinte, although chromosome studies of this section had not been made at the time of Babcock's publication.

Relation of Chromosome Knobs to Geographic Distribution

Reeves (33) reported a relationship between knob number and proximity to Guatemala which was statistically significant at the .05 level, when all of the 163 varieties studied were included in the analysis, and at the .01 level, when all were included except those from the Andean region. This difference in levels of significance indicated that the Andean region occupied some kind of special position in the pattern; that, were it not for samples from this region, the entire relationship would have been significant at the .01 level. Randolph agreed that a correlation was established, but he then questioned the value of the results. Although his objections are ambiguous, the inference is that the correlation observed might be merely one of knob number with low altitude, rather

than with proximity to Guatemala. In rebuttal, it may be stated with certainty that none of the samples were selected because of the altitude of their origin. That the high average knob number for Guatemala is not seriously in error is shown by Reeves' comparison of his samples with those of Mangelsdorf and Cameron (23), for which data on altitude were given. Facts presented in the following paragraph indicate that the relationship observed between knob number and proximity to Guatemala in samples originating in the United States is causal. It is possible that some selectivity for low knob number did occur in the Andean region because of the prevailingly high altitude there, but it is especially noteworthy that the inclusion of the data for this region did not strengthen the observed relationship but rather weakened it. It is, therefore, reasonably clear that the samples were taken from altitudes at random and that altitude was not *per se* responsible for the relationship observed. This conclusion is, of course, based in part on the assumption that there is no positive relationship between low altitude and proximity to Guatemala. If such a relationship does exist, it is not detectable in relief maps, and, in fact, it almost certainly is non-existent. All of these facts are given, and some of them are strongly emphasized, in the literature cited on this topic by Randolph. It is unfortunate that Randolph overlooked these additional facts when he raised his objections.

Longley (18), working with corn of the United States, showed that there exists a pronounced relationship between knob number and proximity to the Mexican border, even when only the high altitude states of Montana, Idaho, Utah, Colorado, Arizona and New Mexico are taken into consideration. Or, if all of the states from which he took samples, regardless of altitude, are considered, there is even then a relationship. Longley rec-

ognized the relationship and mentioned it several times. Weatherwax (51) stated without reservation: "The average number of knobs in maize varieties decreases with the distance north or south from Central America —that is, with distance from the area where contamination with teosinte is most likely to occur." So far as we are aware, Randolph is the only student of this problem who denies the existence of a real correlation between the number of knobs and proximity to the general region of Guatemala.

High knob number has been studied in relation to yield (50, 54) and other plant characters, but this topic will be reviewed in a separate publication (27).

We have never interpreted these correlations as "proof" (32) of recent admixtures of corn and Tripsacum. They are best explained, however, on the assumption that corn not only is older than teosinte but that it was widespread over the hemisphere before teosinte originated in Guatemala. According to this assumption, the knob-bearing chromatin of teosinte diffused through corn in all directions, by hybridization, but the greatest concentration continues to be in the vicinity where teosinte originated and still occurs.

Chromosome Characters of Corn and its Relatives

A great body of literature pertaining to the chromosomes of corn, teosinte and Tripsacum is in existence. Except for the significance of the number and position of knobs, this topic is relatively free from controversy, and the pertinent facts may be stated briefly.

The normal diploid chromosome number of corn is 20, and no stable aberrant numbers are known, although some varieties have supernumerary chromosomes (B-chromosomes) which behave irregularly during meiosis

and are not known to be the bearers of any specific genes. Annual teosinte has 20 chromosomes, the same as corn, and perennial teosinte 40; some varieties of teosinte also have B-chromosomes. The lowest somatic number yet reported for Tripsacum is 36, but forms with 72 have long been known, and others with 45, 54, 90 and 108 have been reported by Farquharson (13). All writers on the subject have thus far continued to designate the 36-chromosome form of Tripsacum as diploid, but most of them, in doing so, probably recognize the possibility that it may be tetraploid.

As to chromosome length and arm ratio, a majority of the corn varieties are essentially similar to one another and may be designated for convenience as "normal." The normal type is described and diagramed by Rhoades (39). Numerous aberrants are also known, some of them resulting from recent structural changes and others being of unknown origin. In these characteristics, the chromosomes of teosinte are usually similar to those of corn, but there are conflicting reports on this question (32). Longley (20) found that the synapsed pachytene homologues of an F_1 corn-teosinte hybrid were not significantly different from each other, and Randolph (32) accepts Longley's results as justification for a final conclusion. However, Brown (6), working with hybrids of an entirely different plant, *Gossypium*, showed that paired pachytene chromosomes of different genom groups are equal in length, despite differential size at metaphase, thus casting some doubt on the decisiveness of Longley's results even before Randolph's paper was published. The chromosomes of Tripsacum are so different from those of corn or teosinte in size and arm ratio as to defy a brief comparison. In general, they are much shorter and show many differences in arm ratio.

The number of chromosome knobs varies in corn, teo-

sinte and Tripsacum according to species and strains, but neither average numbers nor exact ranges in numbers for the various groups have yet been adequately determined. The most recent chromosome-knob count which has come to our attention for *T. dactyloides* (n= 18) is 22 to 26 (32). This is greater than any number yet reported for corn or teosinte, and even if this form of Tripsacum be regarded as tetraploid, its number of knobs per genom of nine chromosomes is greater than the average of either corn or teosinte. As to corn and teosinte, perhaps the statement will stand without contradiction that, broadly speaking, corn has the lowest number and annual teosinte an intermediate number.

As to position of knobs, those of *T. dactyloides* have a strong tendency to be terminal, but Ting (49) has shown that in another form of Tripsacum some of them are obviously intercalary. Most of the knobs of corn are intercalary, but a few are terminal; the most common position is sub-terminal, or at least closer to the end than to the centromere. Annual teosinte is again intermediate; more of its knobs are terminal than in corn, but more are intercalary than in *Tripsacum dactyloides*. Many varieties show pronounced differences in this character; according to Longley (17), the knobs of the Guatemalan varieties from Progresso, Moyuta, Nojoyo and San Antonio Huixta are mostly terminal, but those of the Mexican varieties from Durango and Chapingo are more often intercalary, like those of corn. The intermediate position occupied by teosinte, in both number and position of chromosome knobs, is one of the several characters which may be explained by the view that teosinte is a hybrid combination of knobless, pure corn and a form of Tripsacum similar to *T. dactyloides* with many knobs.

No objection to the view that teosinte occupies an intermediate position in these respects has come to our

attention, and Weatherwax (51) accepts it as a fact. Randolph (31, 32) does point out that *T. maizar* and *T. australe* are knobless or nearly so, and since he assumes that these are the only diploid Tripsacums native to Mexico and Guatemala, he concludes that any species of Tripsacum which might have hybridized with corn to produce teosinte must have been a knobless form. But it has already been explained that there are reasons for the opinion that *T. dactyloides*, or possibly one of its parents, was present in or near Guatemala in prehistoric times.

An objection has been raised (31) that the hybrid origin of teosinte requires its chromosomes to be intermediate between those of its putative parents in length and number. This objection is not valid. What should be expected does occur: the chromosomes of teosinte are similar in length and number to those of its hypothetical recurrent parent, corn. It is also important to note that Maguire's (21, 22) reports of exchanges between corn and Tripsacum chromosomes do not indicate that length and number of chromosomes were affected.

Objections to the hypothesis of the hybrid origin of teosinte have been made (31, 32) on the additional grounds that the chromosomes of teosinte are "so similar to those of corn and so dissimilar to those of Tripsacum that it seems highly improbable an exchange of segments could have occurred on a sufficiently extensive scale to account for the hybrid origin of teosinte . . ." The discussion immediately preceding the section which is here quoted shows that the writer was referring to similarities and dissimilarities in length and arm ratio. But there is no known reason why such differences should prevent the exchange of segments. It is well known, for example, that in heterozygous translocation stocks of corn, chromosomes differing widely in length and arm

ratio do synapse and exchange segments. The fact that corn and Tripsacum can be hybridized betokens some measure of homology between their chromosomes; and if this homology does exist, differences in length and arm ratio need not prevent the exchange of segments. Just how extensive this exchange should be to meet the requirements of the hypothesis of the hybrid origin of teosinte is impossible to estimate. But, if the rate were extensive, in the sense of being unrestricted or only slightly restricted, we should expect corn and Tripsacum to have merged into one continuous though highly variable group, with little or no barrier separating the parental species from each other or from their hybrids.

Weatherwax (53) states that polyembryony, apomixis and chromosomal variation in Tripsacum, as reported by Farquharson, serve to increase the doubt that a corn-Tripsacum cross could have given rise to the "stable and relatively uniform plant that teosinte is." Such an opinion needs some expansion in order to be convincing, for Weatherwax makes no attempt to point out whether or not it is based on any cytological or genetical principle. In its present form, this opinion is another *non sequitur* requiring no further discussion here.

The Transfer of Chromosome Knobs from Tripsacum to Teosinte and Corn

Extensive objections (31, 32) have been raised to our view that chromosome knobs have been transferred from Tripsacum through teosinte to corn, on the grounds that the knobs are mostly terminal in Tripsacum but mostly intercalary in corn, and that such a transfer would require chromosomal rearrangements, for which there is little evidence.

We have stated at least twice (26, 36) that if it were explained how corn, monophyletic as it is sometimes

claimed to be, has come to have different numbers of knob positions without extensive chromosomal rearrangements, perhaps a fraction of the problem of the origin of corn would be solved. But there is as yet no explanation. Longley (19, 20) interpreted his data as supporting the hypothesis of a series of inherited gradients. However, this hypothesis has been discredited by Mangelsdorf and Cameron (23) and by Rhoades (41) in several ways. Rhoades points out, for example, that the interpretation is without experimental evidence and is contradictory to the often observed fact that when a knob is shifted by rearrangement from one position to another its appearance does not change. Randolph (32) contributes a single sentence which constitutes his most positive explanation:

> The present status of the problem concerning differences with respect to the prevalence of terminal and intercalary chromosome knobs in corn, teosinte and Tripsacum forces one to the conclusion that gene mutation rather than hybridization accompanied by structural chromosomal alterations has produced these fundamental differences in chromosome morphology.

He then states that his conclusion is similar to that of Longley (19) but does not sufficiently expand his idea to make it clear and convincing. So far as his explanation goes, it is very well in agreement with the theory that teosinte is a hybrid; it simply means that teosinte is intermediate between corn and Tripsacum for *genes* controlling number and position of chromosome knobs. But Randolph's explanation seems to meet with the same difficulties that Rhoades pointed out with respect to Longley's.

Randolph's (32) favorable attitude towards the view that modern corn is a composite of several wild species of *Zea* might have been intended as a possible explanation of the various knob numbers and positions now known. But even so, it contributes nothing towards a

solution to the problem, for, according to the theory of common ancestry, all corn, as well as teosinte and Tripsacum, is traceable eventually to a single ancestor, even though the line of descent might pass through one or more intermediate ancestral forms. Somewhere in such a line of descent there must have arisen many changes in number and position of knobs. Yet Randolph insists that, according to the tripartite theory, structural rearrangements would be required to account for the different knob positions, without recognizing that they would be required equally by the theory of common ancestry.

A few literature reports will now be mentioned indicating that some varieties of corn contain structural chromosomal differences not usually recognized. Rhoades and Dempsey (42), working on 90 exotic races of corn, did not find indications of large structural differences among races when pollen abortion was used as the index, but they did find significant differences in the amount of crossing over in heterozygotes involving diverse races. Ono and Suzuki (30) found six different karyotypes in 11 corn accessions out of 69 from Nepal, the karyotypes differing in total length or in arm ratio, or both, in certain chromosomes. Blanco (5) reported various structural abnormalities in corn, following self fertilization and subsequent crossing. Clark (9) recognized six translocations and two inversions occurring naturally among the entries in corn-yield tests at the Connecticut Agricultural Experiment Station in a single season.

No final conclusion has been reached, except by Randolph (32), that abnormal chromosome 10 is anything other than the result of a simple attachment of a natural end of chromosome 10 to a fragment of another chromosome. Such an attachment to a terminal knob would change the position of the knob from terminal to inter-

calary and may serve to illustrate a possible mechanism by which some of the knobs which were once terminal became subterminal.

Abnormal chromosome 10 differs from normal chromosome 10 in the greater length of its long arm and in the greater proportion of heteropycnotic chromatin in its distal segment. Longley (17) reported this type of chromosome in corn and Chapingo teosinte and gave two possibilities as to its origin:

> The origin of the much-knobbed, longer types of chromosome X might be the result of the addition of a fragment marked by both a terminal and an internal knob, or the picture might be reversed by considering that the normal short types have resulted from the loss of a terminal portion of the long arm of the long types.

There can be no doubt as to the meaning Longley intended to convey—that one of the two possibilities was the simple addition of a fragment. Longley (18) continued to refer to this type in corn as having "an additional piece on the end of the long arm," without revising his original explanation. It may be noted that Longley's interpretation of the origin of this chromosome was given in 1937, five years after Burnham's (7) discovery that a certain translocation previously reported as simple was in reality reciprocal, and three years after Sharp (44) had stated that Burnham's discovery "naturally raises a question regarding other supposed simple translocations." In other words, Longley's suggestion that abnormal chromosome 10 might be the result of the simple addition of a fragment naturally leads to the inference that he was aware of the widespread belief that broken ends are incapable of attaching themselves to natural ends, but that he regarded this case as an exception to the rule. Randolph himself recently (31, 32) contributed what might be regarded as two different views on the question. In the first paper cited, he states that normal ends "ordinarily" do

not fuse with broken ends; but, in the second paper, published after Reeves (36) had made use of Longley's interpretation as a possible illustration of how terminal knobs might become intercalary, he states: ". . . it is a well-known fact that chromosome fusion occurs only between recently broken ends . . ." And referring to the additional chromatin in abnormal chromosome 10, he states: "It is a segment that has replaced the terminal one-sixth of the long arm of chromosome 10, as Rhoades (40) has clearly shown."

The facts are that Rhoades (38, 40) discussed the question of the origin of abnormal chromosome 10 and later (41) referred to it again, without stating a conclusion. He did point out that a short terminal region of abnormal chromosome 10 has a chromomere pattern differing from that of the corresponding region of normal 10, and that crossing over is reduced in this region. This might indicate that abnormal 10 originated by the replacement of a short terminal segment with a much longer nonhomologous segment. But he pointed out that this explanation would require plants homozygous for abnormal chromosome 10 to be homozygous deficient for certain loci found in the terminal region of normal chromosome 10. This is unlikely, because plants homozygous for abnormal chromosome 10 are not noticeably different in phenotype from their sibs carrying only the normal chromosome 10.

Recently, Ting (48) reported cytological evidence indicating that an abnormal chromosome 10 did originate by simple translocation. A fragment, containing a centromere, of a B-chromosome became attached to the natural end of the long arm of chromosome 10.

In the absence of a completely satisfactory explanation, however, it may be said that the tripartite theory accounts for the fact that the number of knobs in teosinte

is intermediate between the numbers in corn and Tripsacum better than does the theory of common ancestry. It accounts much better for the apparent fact that teosinte is intermediate between corn and Tripsacum, at least in a broad sense, in position of the knobs.

Teosinte Intermediate in Plant Characters

One important category of circumstantial evidence for the hybrid origin of teosinte shows that teosinte has few if any plant characters of its own; it is either intermediate between corn and Tripsacum or similar to one or the other in essentially all of its characters. The significance of this fact has been almost completely overlooked. Randolph (32) makes a fleeting reference to it, but states merely that the "very stable cytological features," which are discussed on previous pages of the present paper, are more important.

Thirty-two characters, in addition to those of chromosome morphology, which usually distinguish corn from Tripsacum, were listed by Mangelsdorf and Reeves (26). Reeves later (35) studied 23 characters, two of which were repetitions of the 32 previously studied. In the 53 characters thus examined, teosinte is either intermediate between corn and Tripsacum or very similar to one of them, with two doubtful exceptions. Teosinte was actually intermediate in one of the characters designated as exceptional—frequency of large leaf hairs—but the differences between corn, teosinte and Tripsacum were not statistically significant, and this character, therefore, does not constitute a true exception. In the other exceptional character—depth of alveolus of the rachis—Tripsacum appeared to be intermediate between corn and teosinte, teosinte having the deepest alveolus of the three. It was recognized that for eight of these characters, the plant samples were too small for completely dependable

results, but even if these eight characters were ignored, which would not be fully justified, 43 characters are left which support the hypothesis of the hybrid origin of teosinte as against one which apparently does not. This single exception—depth of alveolus—might be accounted for in any of several ways, the most plausible being gene interaction.

Mangelsdorf and Reeves (26) stated that neither *T. dactyloides* nor Andean corn was known to have the freely-branching tassel of teosinte and that, in this character, therefore, they would fall short of being satisfactory putative parents of teosinte. Since that time, however, Reeves (34) has pointed out that the tassels of some varieties of Andean corn are very profusely branched. Hence, *T. dactyloides* is not ruled out because it lacks a freely-branching tassel. It should be emphasized that the list of characters studied (26, 35) includes those of the floral organs and inflorescences, which are conventionally recognized in this alliance as generic characters.

This intermediate position of teosinte is a peculiar condition which has not been explained, and which apparently cannot be explained, by divergent evolution of the three taxa from a common ancestor. If the relationship held true for only one or very few characters, it might be dismissed as being of no importance; since it holds for a large number of them, it strongly suggests that teosinte actually inherited its characters from corn and Tripsacum.

Evidence from Fossil and Archaeological Maize

The evidence from both fossil and archaeological remains is best explained by the theory of a hybrid origin of teosinte, for it suggests that teosinte appeared on the scene more recently than either corn or Tripsacum and only after agriculture had become well established.

Barghoorn *et al* (4) identified fossil pollen grains of both corn and Tripsacum isolated from drill cores taken at a depth of more than 69 meters below the present site of Mexico City. Pollen grains thought to be those of teosinte were found also but only at levels above 3.6 meters[2] which were probably laid down after agriculture had become established in the Valley of Mexico. Barghoorn *et al* also point out that teosinte pollen is intermediate between corn and Tripsacum pollen, not only in its diameter but also, and perhaps more significantly, in the ratio of diameter of pore to the long axis. They conclude that this intermediate value is well in harmony with the postulated hybrid origin of teosinte.

Virtually all of the archaeological corn so far studied shows that teosinte introgression, when it can be recognized, made its appearance only after pure corn had been grown for some time. Mangelsdorf and Smith (28) found no evidence of teosinte introgression in the lower levels of Bat Cave, although such introgression was conspicuous in the upper four levels. Cutler's (10) descriptions and illustrations of prehistoric specimens from Tularosa Cave show that the typical corn from the lower pre-pottery levels is non-tripsacoid, while some of the specimens from the higher levels are strongly tripsacoid.

The prehistoric corn from the lower levels of La Perra Cave in Mexico (25) had predominantly non-tripsacoid glumes, while that from the uppermost level had a high proportion of cobs with tripsacoid glumes. The most tripsacoid cob in the entire collection occurred in the highest level.

Mangelsdorf and Lister (24) reported that tripsacoid cobs occur in the upper levels of Swallow Cave in north-

[2] Weatherwax (53) is clearly in error in stating that teosinte pollen was found at depths of more than 150 feet. Randolph, the joint author of the same chapter, correctly states that no teosinte pollen was found at levels below 3.6 meters.

western Mexico and are found in three other caves—Slab, Tau and Olla—in the State of Chihuahua. Non-tripsacoid maize resembling a Mexican race, Chapalote, was found in the lower levels of Swallow Cave.

Galinat *et al* (16) found tripsacoid cobs to be quite common among the prehistoric specimens from Richards Cave and Tonto Cave in Arizona. Both sites are regarded as relatively late. Galinat (unpublished) found also that the early maize from Cebollita Cave in New Mexico is not tripsacoid, while later maize includes many specimens showing teosinte introgression.

The six studies on archaeological maize reviewed above, only one of which was known to Weatherwax and Randolph, as well as the data on fossil pollen, support the theory that teosinte, because it is a hybrid of Tripsacum and cultivated maize, came into existence only after the cultivation of maize was well established.

Taxonomic Status of Teosinte

When the transfer of the two species of *Euchlaena* to the genus *Zea* was published (37), it was made clear, we believe, that our previous conclusion as to the origin of teosinte did not influence our conviction that the groups should be made congeneric—that the transfer was justified regardless of the manner of the origin of teosinte or corn. Weatherwax (52, 53) and Randolph (31, 32) have overlooked or ignored these statements and have repeatedly confused the taxonomic change with the issue of the origin of teosinte. If we could agree with their theory that corn and teosinte originated by divergent evolution, our conviction that the two groups ought to be regarded as congeneric would not be weakened in the least.

Randolph himself (32) recognizes that hybrid intergrades between corn and teosinte do occur naturally and describes the intergradation as occurring in the very same

characters which he contends are stable and of generic value. He recognizes also that their cytogenetical relationships really approach those of a single species. He reaches the somewhat conflicting conclusions that the characters by which corn and teosinte differ are generic; but that teosinte is maintaining its identity as a "good species." His statement that corn and teosinte are more distinct entities than many other genera of the grass family is vague, and he offers no examples of such genera. Numerous examples are on record of separate genera comprising certain species which are scarcely distinct. To mention only one such case: Fisher, Bashaw and Holt (15) found *Pennisetum ciliare* (L.) Link and *Cenchrus setigerus* Vahl. to be nearly or quite inseparable by either morphological or cytological characters and suggested that the forms examined belong to a single agamic complex, but by no means did they indicate satisfaction with the present taxonomic status of this group. It may be safely stated that plant taxonomists generally are dissatisfied with the classification of such groups. The reason why solutions have not yet been offered for these confusing complexes is that they have not been worked out.

Various degrees of approval of the consolidation of *Zea* and *Euchlaena* have been brought to our attention, although we have not canvassed the literature for examples of this. Sharp (45) reviews the salient facts and states: "This indicates a degree of cytological and genetical similarity unusually high for plants assigned to different genera." Stebbins (47) refers to teosinte as *Zea* (*Euchlaena*) *mexicana*, and Celarier (8) takes a strong position that the transfer is justified. Rollins (43), after reviewing the evidence relative to this problem, states that the two groups are congeneric and that Reeves and Mangelsdorf have rightly transferred *Euchlaena* to *Zea*. Darlington (12) goes even further and insists that *Zea*

and *Euchlaena* ought to be made conspecific, an idea which we had earlier (37) considered but rejected, giving our reasons for doing so. Darlington does not seem to be aware of our publication. Sinnott, Dunn, and Dobzhansky (46) refer to annual teosinte as *Zea mexicana* without reservation. In view of the above facts, Weatherwax's (53) statement that our "proposal has met with little favor" is somewhat erroneous to say the least.

The actual issue involved is whether or not natural relationships as indicated by cytogenetical behavior and gene exchange without the use of artificial techniques are to be recognized in taxonomic treatments. If they are to be recognized, there can be no doubt that the consolidation of *Zea* and *Euchlaena* is justified.

Summary

The circumstantial evidence that teosinte originated as a hybrid between corn and Tripsacum is substantially stronger now than in 1939, when the idea was first proposed, for the following reasons: Not only has the cross between corn and Tripsacum been successfully repeated, but it has been made without special techniques. The species of Tripsacum (*T. dactyloides*) which has come nearest to showing introgression with corn under experimental control has been reported in Guatemala, where teosinte is believed to have originated and where corn is known to have been abundant since ancient times. There is increasing evidence, also, that *T. dactyloides* or forms similar to it, previously were more common in the area than they are now.

Tripsacum genes have been demonstrated to have a phenotypic effect in corn-Tripsacum hybrids, a natural supposition which was once doubted by some students of this problem. The first report of crossing over between

corn and Tripsacum chromosomes, when associated in the same nucleus, has been confirmed.

With few exceptions, annual teosinte, the species most comparable to modern corn, proves to be intermediate between corn and Tripsacum in number and position of chromosome knobs.

It has become increasingly clear that a correlation exists in corn varieties between frequency of chromosome knobs and proximity of their native locality to Guatemala and southern Mexico. As corn and teosinte hybridize naturally, this correlation constitutes further circumstantial evidence on the phylogenetic relationship between corn and teosinte. It is explicable on the assumption that pure corn without knobs was already widespread over the American continent when teosinte originated. Later corn and teosinte began hybridizing, and, in fact, are still doing so; in this way, a slow "diffusion" of corn with knob-bearing chromosomes from Guatemala and southern Mexico has been occurring for several centuries, but an equilibrium in knob frequency throughout the continent has not been reached.

The hypothesis of the hybrid origin of teosinte has been vigorously challenged on the grounds that many of the chromosome knobs of corn are intercalary, whereas those of Tripsacum are terminal, and that changes in knob positions would require structural chromosomal rearrangements which probably have not occurred. Structural rearrangements not previously recognized have been demonstrated since 1939, however, and some forms of Tripsacum actually have been shown to possess a few internal knobs. In any event, our statement of 1939 still stands: that the theory of common ancestry is confronted with this same problem as to the origin of the different knob positions.

Considerable evidence from archaeology and paleo-

botany pertinent to the relative ages of corn, teosinte and Tripsacum indicate that teosinte is of recent origin. This also can be explained by the theory that teosinte originated as a hybrid between corn and Tripsacum.

It should be emphasized that all the facts discussed above are not merely in *agreement* with the theory of the hybrid origin of teosinte, but also that they are *explained* by this theory. The odds are extremely low that a theory can explain so many facts, drawn from so many sources, without being somewhat of an approximation of the truth. Although other current theories are not completely disproved, they do not explain so many of the facts.

The question of whether or not teosinte should be regarded as generically distinct from corn is not a part of the problem of the origin of corn or teosinte. The known facts indicate, however, that the relationship conforms best to that of congeneric species.

LITERATURE CITED

1. Anderson, E., 1944. Cytological observations on *Tripsacum dactyloides*. Ann. Missouri Bot. Gard. 31: 317–323.

2. Babcock, E. B., 1947. The genus Crepis. Univ. California Publ. Bot. 22: 199–1030.

3. ——, 1947. Cytogenetics and speciation in Crepis. Advances in Genetics 1: 69–93.

4. Barghoorn, E. S., M. K. Wolfe and K. H. Clisby, 1954. Fossil maize from the Valley of Mexico. Bot. Mus. Leafl. Harvard Univ. 16: 229–240.

5. Blanco, J. L., 1948. Anormalidades meioticas en relacion con la consanguinidad en *Zea mays* L. Consejo Superior de Investigaciones Cientificas, Mision Bioloica de Galicia, Madrid.

6. Brown, M. S., 1954. A comparison of pachytene and metaphase pairing in species hybrids of *Gossypium*. Genetics 39: 962–963.

7. Burnham, C. R., 1932. An interchange in maize giving low sterility and chain configurations. Proc. Nat. Acad. Sci. 18: 434–440.

8. Celarier, R. P., 1957. Cytotaxonomy of the Andropogoneae II. Subtribes Ischaeminae, Rottboellinae and the Maydeae. Cytologia 22: 160–183.

9. Clark, F. J., 1942. Cytological and genetical studies of sterility in inbreds of similar and diverse genetic origin. Connecticut Agric. Exp. Sta. Bull. 465.

10. Cutler, H. C., 1952. A preliminary survey of plant remains of Tularosa Cave. Fieldiana: Anthropology (Chicago Nat. Hist. Mus.) 40: 461–479.

11. —— and E. Anderson, 1941. A preliminary survey of the genus Tripsacum. Ann. Missouri Bot. Gard. 28: 249–269.

12. Darlington, C. D., 1956. Chromosome botany. London, Allen and Unwin.

13. Farquharson, L. I., 1955. Apomixis and polyembryony in *Tripsacum dactyloides*. Amer. Jour. Bot. 42: 737–743.

14. ——, 1957. Hybridization in Tripsacum and Zea. Jour. Hered. 48: 295–299.

15. Fisher, W. D., E. C. Bashaw and E. C. Holt, 1954. Evidence for apomixis in *Pennisetum ciliare* and *Cenchrus setigera*. Agron. Jour. 46: 401–404.

16. Galinat, W. C., P. C. Mangelsdorf and L. Pierson, 1956. Estimates of teosinte introgression in archaeological maize. Bot. Mus. Leafl. Harvard Univ. 17: 101–124.

17. Longley, A. E., 1937. Morphological characters of teosinte chromosomes. Jour. Agric. Research 54: 835–862.

18. ——, 1938. Chromosomes of maize from North American Indians. Jour. Agric. Research 56: 177–196.

19. ——, 1939. Knob positions on corn chromosomes. Jour. Agric. Research 59: 475–490.

20. ——, 1941. Knob positions on teosinte chromosomes. Jour. Agric. Research 62: 401–413.

21. Maguire, M. P., 1952. Synapsis and crossing over of Tripsacum and Zea chromosomes derived from hybrids backcrossed to Zea. Ph. D. Thesis, Cornell University.

22. ——, 1957. Cytogenetic studies of Zea hyperploid for a chromosome derived from Tripsacum. Genetics 42: 473–486.

23. Mangelsdorf, P. C. and J. W. Cameron, 1942. Western Guatemala, a secondary center of origin of cultivated maize varieties. Bot. Mus. Leafl. Harvard Univ. 10: 217–252.

24. —— and R. H. Lister, 1956. Archaeological evidence on the evolution of maize in northwestern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 151–178.

25. ——, R. S. MacNeish and W. C. Galinat, 1956. Archaeological evidence on the diffusion and evolution of maize in northeastern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 125–150.

26. —— and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exp. Sta. Bull. 574.

27. Mangelsdorf, P. C. and R. G. Reeves, 1959. The origin of corn III. Modern races the product of teosinte introgression. Bot. Mus. Leafl. Harvard Univ. 18 : (In press).

28. — — and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harvard Univ. 13 : 213–247.

29. Melhus, I. E., 1953. A preliminary study of the diseases of corn and some related hosts in Guatemala. Iowa State College Jour. Sci. 27 : 519–536.

30. Ono, T. and H. Suzuki, 1956. Chromosomes of maize. Land and crops of Nepal Himalaya 2 : 365–372.

31. Randolph, L. F., 1952. New evidence on the origin of maize. Amer. Nat. 86 : 193–202.

32. ——, 1955. History and origin of corn II. Cytogenetic aspects of the origin and evolutionary history of corn. *In* Corn and corn improvement : 16–61. New York, Academic Press.

33. Reeves, R. G., 1944. Chromosome knobs in relation to the origin of maize. Genetics 29 : 141–147.

34. ——, 1950. Morphology of the ear and tassel of maize. Amer. Jour. Bot. 37 : 694–704.

35. ——, 1953. Comparative anatomy of the American Maydeae. Texas Agric. Exp. Sta. Bull. 761.

36. ——, 1953. New "evidence" on the origin of maize. Amer. Nat. 87 : 157–159.

37. —— and P. C. Mangelsdorf, 1942. A proposed taxonomic change in the tribe Maydeae (family Gramineae). Amer. Jour. Bot. 29 : 815–817.

38. Rhoades, M. M., 1942. Preferential segregation in maize. Genetics 27 : 395–407.

39. ——, 1950. Meiosis in maize. Jour. Hered. 41 : 59–67.

40. ——, 1952. Preferential segregation in maize. *In* Heterosis : 66–80. Iowa State College Press.

41. ——, 1955. The cytogenetics of maize. *In* Corn and corn improvement : 123–319. New York, Academic Press.

42. Rhoades, M. M. and E. Dempsey, 1953. Cytogenetic effects of deficient-duplicate chromosomes derived from inversion heterozygotes in maize. Amer. Jour. Bot. 40: 405–424.

43. Rollins, R. C., 1953. Cytogenetical approaches to the study of genera. Chronica Botanica 14: 133–139.

44. Sharp, L. W., 1934. Introduction to cytology. 3rd ed. New York, McGraw-Hill.

45. ——, 1943. Fundamentals of cytology. New York, McGraw-Hill.

46. Sinnott, E. W., L. C. Dunn and Th. Dobzhansky, 1958. Principals of genetics. 5th ed. New York, McGraw-Hill.

47. Stebbins, G. L., Jr., 1950. Variation and evolution in plants. New York, Columbia University Press.

48. Ting, Y. C., 1958. On the origin of abnormal chromosome 10 in maize (*Zea mays* L.). Chromosoma 9: 286–291.

49. ——, 1959. Internal knobs on the chromosomes of two tropical forms of Tripsacum. Maize Gene Coöp News Letter 31: 72.

50. Vachhani, M. V., 1950. A study of the relationship of chromosome knobs with certain agronomic and morphological characters in corn inbreds. Agron. Jour. 42: 196–201.

51. Weatherwax, Paul, 1950. The history of corn. Sci. Month. 71: 50–60.

52. ——, 1954. Indian corn in old America. New York, Macmillan.

53. ——, 1955. History and origin of corn I. Early history of corn and theories as to its origin. *In* Corn and corn improvement: 1–16. New York, Academic Press.

54. Wellhausen, E. J., A. Fuentes O. and A. Hernandez C., *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize in Central America. Nat. Acad. Sci.—Nat. Res. Council Publ. No. 511.

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THE ORIGIN OF CORN
III. MODERN RACES, THE PRODUCT OF TEOSINTE INTROGRESSION

BY

PAUL C. MANGELSDORF AND ROBERT G. REEVES

THE third postulate of our tripartite hypothesis (35) that certain modern races of maize are the product of teosinte (*Zea mexicana*) introgression has been the least controversial of the three. There is now almost unanimous agreement among those who have studied the problem that corn and teosinte are constantly hybridizing in Mexico and Guatemala and that this introgression of one species into the other necessarily has had substantial genetic effects. The exception to this unanimity is represented by Randolph (41) who has offered the following objections: (A) There is little natural crossing between maize and teosinte. (B) The extent to which hybridization between the two species has resulted in gene exchange is open to question. (C) There is no cytological evidence of the introgression of teosinte into maize. (D) There is no evidence that introgression, if it occurs, leads to improvement. (E) Characters found in maize varieties which have been attributed to teosinte introgression can be equally well explained as the result of parallel mutations.

How valid are these objections and to what extent are they supported by the evidence?

The first objection is plainly contrary to the facts. It may be true, as Randolph suggests and as others have recognized (8), that there are partial genetic barriers to the free hybridization of corn and teosinte in nature. Certainly the number of recognizable hybrids found in localities where the two species are growing together in the same fields, and flowering at the same time, is less than might be expected in view of the fact that both species are monoecious and wind pollinated and that abundant opportunities for hybridization apparently exist. But the barriers, whatever their nature, are by no means complete, and every student of the problem from Harshberger on has been aware of natural hybridization of corn and teosinte (8, 16, 18, 30, 41). Randolph, himself, has furnished the most convincing evidence of this hybridization, when he counted 45 F_1 hybrids in five days of travel in a limited region near the villages of Nojoyá and San Antonio Huixta in Guatemala. If this small sample is representative, there must be thousands of new hybrids produced each year. That Randolph personally failed to find hybrids near Chalco in Mexico is of no significance, for others (18, 30) have done so.

That maize and teosinte hybridize in Mexico and Guatemala must be accepted as an established fact and, if the frequency of that hybridization is less in any one place at any one time than some botanists expect, it must be remembered that it has been going on in countless localities for many centuries.

The extent to which this hybridization results in gene exchange is not easily measured with precision, but it cannot be denied that there is some exchange. This would be expected on the basis of the following well-established facts: (a) The F_1 hybrids of corn and teosinte are usually vigorous and highly fertile and are easily backcrossed to either parent to produce fertile progeny; (b) The chro-

mosomes of the two species are morphologically similar and synapse more or less normally in the hybrids (2, 3, 4, 19, 20, 21); (c) The arrangement of the gene loci although probably not identical in the two species is certainly similar (11); (d) Crossing over between linked loci in maize and teosinte chromosomes is, with few exceptions, of the same order as it is in corn (11). In view of these facts, it is difficult to see how, once hybridization has occurred, gene exchange could be prevented; and there is ample evidence that it has not been.

Collins (8) noted many years ago that the teosinte in the vicinity of Chalco in Mexico is quite maize-like in its characteristics, including plant color and pilosity of the sheaths. The first of these characters involves at least one gene either *B* or *R* and the second at least two (39). In being transferred from maize to teosinte, these genes have undoubtedly carried with them blocks of closely linked genes which accounts, at least in part, for the fact that the teosinte of Chalco is among the most maize-like varieties in many other respects. Randolph (41), himself, has found yellow endosperm, a maize character, in teosinte, and Mangelsdorf (28) has reported both yellow endosperm and colored aleurone.

There is no doubt that the teosinte of Mexico is more maize-like than that of Guatemala in its general aspects (18), in cytological features (21, 24, 25) and in genetic characteristics (47, 48, 49). Reeves (44) found a hybrid of the Mexican teosinte Nobogame x New to have uniformly paired spikelets, a so-called "generic" character of *Zea*, distinguishing it from teosinte. These facts require explanation, and the simplest and most commonly accepted one is that the Mexican teosintes have, on the average, undergone more admixture with maize than have the Guatemalan varieties. Longley's explanation of the cytological differences as the product of "gradi-

ents" has been pretty thoroughly demolished (32, 45).

Since some varieties of teosinte have obviously been modified by admixture with maize, it is almost inevitable that some varieties of maize have likewise been modified by admixture with teosinte. Weatherwax concedes this in the same chapter in which Randolph attempts to deny it. And if this conflict of opinions proves to be confusing to some readers, it at least demonstrates an admirable independence of mind on the part of the two joint authors.

Wellhausen *et al* (53), in an important paper which both Weatherwax and Randolph have repeatedly overlooked, report the results of an intensive study, over a period of seven years, of more than 2000 collections of maize from all parts of Mexico. Of the 25 races of maize which they describe, they recognize teosinte introgression in 22, primarily on the basis of the induration of the rachis and the lower glumes of the ears. Their scores for teosinte introgression proved to be strongly correlated with chromosome knob number; and more recently, they have shown a remarkable correlation with resistance to a virus disease, corn "stunt" (7). Here may be another case, similar to that reported by Venkatraman and Thomas (57), of one of the lower forms of life being more perceptive than botanists in recognizing the true nature of populations.

Randolph's conclusion that there is no cytological evidence of the introgression of teosinte into maize is correct only if his assumption that the chromosome knobs of maize are not derived from teosinte is valid. But apart from chromosome knobs, what cytological evidence of introgression could there be? Randolph has repeatedly emphasized the remarkable similarity, except for the knobs, between maize and teosinte chromosomes. If they are indeed as similar as he regards them to be, then even

the most extensive introgression of teosinte into maize would not be detectable, and the lack of cytological evidence of which he speaks would have no significance. On the other hand, if our assumption is valid—that the chromosome knobs of maize have been derived from teosinte and are good indicators of teosinte admixture—then there is abundant cytological evidence of teosinte (or Tripsacum) introgression in the maize varieties of practically all parts of this hemisphere (5, 32, 42, 46, 53).

There is no longer any doubt that the knobs of teosinte can be transferred to corn. Cytological studies by Ting (unpublished) of the modified strains of inbred A158 developed by Mangelsdorf have shown that knobs have been introduced into various modified strains from chromosomes 1, 2, 3, 5, 8 and 9 of Durango teosinte and from chromosome 4 of Nobogame teosinte.

Nor can there be any doubt that chromosome knobs are associated with tripsacoid characters. Mangelsdorf and Cameron (32) showed that in the maize of western Guatemala the number of chromosome knobs is associated with several characteristics which may have been derived from Tripsacum, including denting of the kernels, fibrous seminal roots, and resistance to shattering, lodging, and smut infection. Brown (5) found high knob numbers to be positively correlated with high row numbers, denting, absence of husk leaves, many seminal roots and irregular rows of kernels, all of which are characteristic of Southern Dents; but he concluded that more data are needed before chromosome knobs can be regarded as reliable indicators of Tripsacum germplasm, since the Northern Flints, apparently the most tripsacoid maize in the United States, have the lowest knob number. Brown added a comment, however, which Randolph, in discussing the results, seems to have overlooked, that the tripsacoid nature of Northern Flints

may be a superficial one. This is probably the case. We expressed the opinion some years ago (36) that the flint-flour corns of the Plains Indians, some of which are included in Brown's Northern Flints, show little admixture with Tripsacum in spite of their straight rows. Additional experience has confirmed this earlier impression. The origin of the Northern Flints is still obscure, but the corn in Latin America which most resembles them occurs at high altitudes in Guatemala, is non-tripsacoid, and has low chromosome knob numbers (55).

The question whether or not corn is improved by teosinte introgression is answered in part by circumstantial and in part by direct evidence. Vachhani (56) found no correlation between chromosome knob number and various morphological and agronomic characteristics, including yield, in 20 inbred strains, but added that these results are not necessarily in conflict with those of Mangelsdorf and Cameron since only relatively low knob numbers were involved. Three additional papers (overlooked by Randolph) contain evidence which suggests or shows that teosinte introgression, in some instances at least, results in improvement.

Wellhausen *et al* (53) concluded that the more productive races of maize in Mexico had undergone introgression from teosinte and that some of the most valuable races, such as Tuxpeño and Celaya, are the product of several independent introductions of teosinte germplasm into maize. More recently, Wellhausen and Prywer (54) showed that among inbred lines developed from Mexican varieties adapted to elevations from 4500 to 6000 feet, those with the higher knob numbers tended to be the parents of the more productive hybrids. The reverse was true at higher altitudes. These results are consistent with those of Mangelsdorf and Cameron which showed that, in Guatemala, teosinte introgression is slight at altitudes

of more than 6500 feet presumably because it confers no advantage at these elevations. Wellhausen and Prywer's conclusion is as follows:

> . . . these data suggest that there is a relationship between knob number and yield factors. At low altitude, the high-knobbed inbred lines tend to be better combiners than the low-knobbed ones. At high altitudes, the reverse seems to be true; the low-knobbed lines tend to be the best combiners. It is now almost certain that many of the good, high yielding, open-pollinated varieties in Mexico during their evolution picked up some favorable characters from teosinte or *Tripsacum*. The number of knobs a variety has may well be indicative of the amount of germplasm it has received from these two species.

It is possible that the Indians of western Mexico have long recognized the beneficial effect of teosinte introgression, for Lumholtz (27) reported their practice of interplanting *maizillo* (probably teosinte) and maize for the purposes of improving the latter. This, however, is quite in contrast with the attitude of the natives of the Valley of Mexico who contend that the presence of teosinte plants in the field causes the maize to "run down." Here again it may be a matter of altitude.

The question may be raised whether or not the introgression of teosinte into maize which has occurred in Mexico and Guatemala has any influence on corn beyond the borders of these countries. There is little doubt that it has. Practically all of the corn varieties of the United States owe their origin to Mexican and Guatemalan races. The Corn-Belt Dent, the principal type in the United States, is a hybrid of the Southern Dents and Northern Flints (1). The Southern Dents in turn are derived from Mexican lowland corns (6) which are highly tripsacoid races believed to be the product of teosinte introgression (53).

The only direct evidence of the improvement effected by controlled introgression of teosinte is furnished by the data of Reeves (43), who introduced teosinte germplasm

into two Texas inbred strains, 4R3 and 127C. Some of the modified strains of 4R3 showed significantly greater tolerance to heat than the controls but were not appreciably changed with respect to yielding ability of their hybrids. Similar modification of 127C, however, increased the yielding ability of its hybrids quite significantly. Reeves concluded that some inbreds can be improved by the addition of teosinte genes but others can not. He postulated that, so far as yield is concerned, 4R3 already has the optimum assortment of teosinte genes. He might have added that 4R3 is actually one of the most tripsacoid inbreds in the United States.

The contention that the tripsacoid characters found in maize varieties can be attributed to parallel mutations rather than to admixture with teosinte has no foundation in the evidence now available. It merely substitutes an untestable hypothesis for the well-established fact that maize and teosinte are hybridizing today and have probably been doing so for almost 2000 years as the evidence from prehistoric corn shows.

Archaeological Evidence of Teosinte Introgression

Virtually all of the archaeological maize from Mexico and North America which has been studied recently includes specimens which are highly tripsacoid and which are quite similar in their general appearance and certain botanical characteristics to modern ears derived from experimental maize-teosinte hybrids. This is especially true with respect to the induration and lignification of the glumes which are known from genetic studies to be among the most common and conspicuous effects of the introduction of teosinte germplasm into maize. Mangelsdorf, for example (28), has shown that the genes for indurated glumes occur on at least four chromosomes of

Nobogame teosinte and on at least five chromosomes of Durango teosinte. Rogers (48) has found linkages between glume score, which is mainly concerned with induration, and marker genes in hybrids involving five varieties of teosinte, the strongest linkage in four of the five hybrids being with the marker gene on chromosome 4. In view of these facts, the occurrence of highly lignified specimens of prehistoric cobs immediately raises the suspicion of previous contamination with teosinte. When lignification is accompanied, as it is in some specimens, with single spikelets, also a teosinte characteristic, the suspicion virtually becomes a fact.

Tripsacoid prehistoric maize was first clearly recognized in a collection of archaeological corn from Bat Cave, a rock shelter in New Mexico excavated by Mr. Herbert Dick (37). Weatherwax (52) was skeptical of this evidence and, since he had seen illustrations of only a limited number of specimens, his skepticism may have been warranted. The data are however quite convincing. Of the 471 cobs studied, 250 or more than half were scored as being intermediate or strong in teosinte introgression. The fact that all but two of these were found in the four upper levels of the deposit was regarded as highly significant and as an indication that teosinte admixture appeared on the scene only after maize cultivation had become well established in the area in which Bat Cave is located.

The second expedition to Bat Cave by Mr. Dick turned up many additional tripsacoid specimens not yet described and has confirmed one of the most significant features of the collection from the first expedition: non-tripsacoid cobs in the early levels, a high frequency of tripsacoid cobs in the later ones.

In addition to those found in the two Bat Cave expeditions, tripsacoid cobs have now been identified in collections from the following caves: Richards and Tonto

Caves in Arizona (14); La Perra Cave in northeastern Mexico (34); Swallow, Tau, Slab, and Olla Caves in northwestern Mexico (33); Cebollita Cave in New Mexico (Galinat unpublished). Additional collections not yet studied but obviously containing tripsacoid cobs have been received from Mr. Herbert Dick from a site in Colorado; from Mr. Dick Shutler from sites in Nevada; and from Dr. Robert E. Bell from a site in Oklahoma. Highly tripsacoid cobs can also be recognized in a photograph of prehistoric specimens from Tularosa Cave in New Mexico published by Cutler (9) and in the illustration of specimens from the Hueco Mountain Caves in Texas published by Cosgrove (cf. 14).

That these tripsacoid cobs are the result of teosinte admixture, which probably occurred in northern Mexico, and not of parallel mutations is strongly indicated by the fact that some of them have more than one character of teosinte, such as distichous spikes, single spikelets and highly lignified rachises and glumes. Simultaneous mutations producing all of these tripsacoid characters are difficult to imagine, but genetic recombinations involving all of them are common in segregates from maize-teosinte hybrids. Both Mangelsdorf (28) and Rogers (48) have shown that there is genetic linkage between all of these characteristics.

Perhaps the strongest evidence that these prehistoric tripsacoid cobs are the product of admixture with teosinte lies in the fact that virtually all of them can be matched quite closely, sometimes almost exactly, with modern specimens derived from experimental maize-teosinte hybrids. Galinat *et al* (14) have illustrated a number of these matched pairs, and we have many others. Until it can be shown that there are other and better ways of synthesizing facsimiles of the tripsacoid prehistoric specimens, we shall continue to assume that

the striking resemblances between the prehistoric and modern specimens reflect a corresponding similarity in their genotypes.

Archaeological Evidence of Improvement

These prehistoric tripsacoid specimens not only show that corn crossed with teosinte centuries ago but they also indicate that corn was improved as a result of the admixture. In all of the collections of archaeological maize in which the lower levels comprise non-tripsacoid corn this early corn is small and uniform in type. In higher levels, accompanying the appearance of tripsacoid types, there is an almost explosive increase in variability. This is especially well illustrated in the collections from Bat Cave in New Mexico (37) and from Swallow Cave in northwestern Mexico (33). This increased variability, which involves types both poorer and better (by modern corn-breeding standards) than the original corn, can be attributed both to genetic recombination and to heterosis. This is especially well shown by the data presented by Galinat *et al* (14), based on 433 specimens in which a high correlation, 0.859, was found between length of cob and estimated teosinte introgression. The correlation is strongly curvilinear, both the shortest and the longest cobs being highly tripsacoid. This is explained by assuming that the short, strongly tripsacoid cobs are homozygous for genes introduced from teosinte, while the long cobs are heterozygous for such genes and are the vigorous products of maize-teosinte heterosis.

It is improbable that the large modern ear of corn could have evolved except for hybridization of corn with teosinte which contributed genes for induration and lignification of the tissues characteristic of the prehistoric tripsacoid specimens. On this point Mangelsdorf (29) has expressed the following conclusion:

The elements of strength necessary to support this greatly enlarged inflorescence have come from teosinte, which contributes genes for hardness and toughness when it is hybridized with corn. Teosinte is to the modern ear of corn what steel is to the modern skyscraper.

The Mutagenic Effects of Teosinte Introgression

Hybridization of maize and teosinte not only produces new genetic combinations, some of which are favorable, but it also has mutagenic effects. These have been recently described by Mangelsdorf (31). Most of the mutations, like spontaneous mutations or mutations produced by irradiation, are deleterious, but some appear to be beneficial. It is entirely possible that these mutagenic effects of teosinte introgression have been an important factor in the evolution of cultivated corn, as important perhaps as the creation of new genetic combinations following hybridization.

Introgression Directly from Tripsacum

After carefully examining the objections to the idea of teosinte introgression, as well as the evidence supporting it, we see no reason to doubt that corn is undergoing introgression from teosinte now and that this process has been going on for centuries. If teosinte is, as we have postulated (35), a hybrid of corn and Tripsacum, then the introgression is ultimately from Tripsacum. We have not assumed that there has been any direct introgression of Tripsacum into maize; our assumption has been that the hybridization of maize and Tripsacum which gave rise to teosinte needed to have occurred only once (35). Evidence is now accumulating, however, to indicate that maize may have hybridized directly with Tripsacum repeatedly, although only once did such hybridization produce teosinte. The evidence for this is of two kinds: (a) tripsacoid characteristics in races of maize which have not

been in obvious contact with teosinte; (b) chromosomes with tripsacoid effects extracted from races of maize far removed from contact with teosinte.

Evidence in the first category is provided by the studies of Roberts *et al* (46), on races of maize of Colombia, especially the race called Chococeño which they describe as follows:

> Chococeño is one of the most unusual races of this hemisphere, both in its characteristics and in the primitive way in which it is grown. Its culture is largely confined to the humid coastal region of western Colombia, where rainfall sometimes exceeds 400 inches annually. The maize is grown without cultivation. The fields are prepared by cutting down the small trees and brush. The seed, which is broadcast and not covered, germinates on the surface of the soil. The plants grow up through the branches of the cut vegetation.
>
> To succeed under these primitive conditions the maize must have unusual characteristics. Chococeño is highly tripsacoid. It has tough, slender stalks with tillers, narrow, drooping leaves and pendulous tassel branches. It has the general aspect of certain segregates from maize-teosinte or maize-Tripsacum hybrids. Since teosinte does not occur in this region, and Tripsacum is common, it has been assumed that Chococeño is the product of the hybridization of maize and Tripsacum.

Roberts *et al* also report that in the Chocó region, from which this peculiar race derives its name, plants of maize and Tripsacum often grow together in the same field and flower at the same time. In a preliminary experiment, varieties of Tripsacum collected in Colombia were crossed with a number of different races of maize, and hybrid seeds, some of them capable of germinating without embryo culture, were produced in all crosses.

All the evidence is consistent with the conclusion that maize and Tripsacum have hybridized in Colombia to produce, not teosinte, but a highly tripsacoid race of maize which, in its vegetative characters, at least, shows some resemblance to teosinte.

Even more tripsacoid, at least in characteristics of the

ear, are some of the specimens of "Maíz Amargo" from the province of Entre Rios in Argentina, collected and described by Ing. Urbano Rosbaco (50). When grown in Massachusetts, plants of this maize, like those of Chococeño of Colombia, have numerous tillers, hispid leaf sheaths and thick, drooping leaves. In Argentina, Maíz Amargo is somewhat resistant to the attacks of grasshoppers, and this fact, coupled with the resemblance of some of its ears to segregates of maize-teosinte and maize-Tripsacum hybrids, led Ing. Rosbaco to suspect contamination with Tripsacum, perhaps the South American species *T. australe*. Horovitz and Marchioni (17) had earlier suggested that the resistance of Maíz Amargo to grasshoppers may be due to Tripsacum introgression.

There is still some confusion about the origin of Maíz Amargo. Rosbaco mentioned several references to it which state that it was introduced into Argentina from the maize-growing region of the Danube. Rosbaco considers this unlikely, and, since the tripsacoid segregates are extremely late in maturity, it does not seem possible that they could have been introduced from the Danube region, to which only varieties of relatively early maturity are adapted, although the original variety which subsequently became contaminated with Tripsacum may have been. *T. australe* has not been reported from Argentina, but it has been collected in the Paraná River basin in Paraguay, not far north of Entre Rios (10).

We have only one determination of chromosome knob number in Maíz Amargo which shows it to be low, five. This is the lowest knob number which we have found in any tripsacoid maize and is consistent with the hypothesis of introgression from *T. australe*, which has been reported to have knobless chromosomes (15) or, occasionally in some forms, a small number of chromosome knobs. Ting (unpublished) has found up to six knobs

in a Colombian Tripsacum believed to be a form of *T. australe*.

We have through repeated backcrossing to inbred A158 extracted from Maíz Amargo a chromosome which has almost the same effects upon the lignification of the pistillate glumes as chromosome 4 of teosinte. Other examples of extracted tripsacoid chromosomes are described below.

Extraction of Tripsacoid Chromosomes from Latin-American Varieties

Chromosomes having effects similar to teosinte chromosomes have been extracted through repeated backcrossing to the inbred A158 from the living varieties of maize of various countries of this hemisphere (31). Modified strains of A158 containing these extracted chromosomes are virtually indistinguishable from those produced by introducing chromosomes directly from teosinte. Furthermore, these extracted chromosomes, like the chromosomes from teosinte, are mutagenic when incorporated into A158 and, more significant still, some of the mutations produced are genetically identical with those produced by teosinte chromosomes. Chromosomes with tripsacoid effects have now been extracted from varieties of corn from Mexico, Honduras, Nicaragua, Cuba, Venezuela, Brazil, Paraguay, Bolivia and Argentina. Those extracted from varieties from Mexico, Honduras and Nicaragua can be attributed to teosinte introgression. Those from Cuba and Venezuela may also be the product of teosinte introgression, for, although there is no teosinte in these countries, there has been some introduction of Mexican and Central American maize varieties. But the tripsacoid chromosomes from Brazil, Paraguay, Bolivia and Argentina come not only from countries where teosinte is unknown but from races of

maize which have no counterparts in the maize of Mexico and Central America. The fact that Farquharson (12) found a variety of Peruvian corn to be especially effective in crossing with Tripsacum is of particular interest in this connection since it suggests the possibility that in some South American varieties the barriers to hybridization with Tripsacum may be weak or lacking.

Conclusions

A careful study has been made of the objections raised against the theory that many modern races of corn are the product of teosinte introgression, and of the new evidence which has been marshalled since the theory was first proposed. Nothing has been found which is clearly in conflict with the theory, whereas the body of facts in support of it is almost overwhelming. We regard this part of the tripartite theory as now so well established that it can safely be employed by corn breeders as a working principle in developing new methods for the improvement of corn.

Summary

Five objections to the theory that many modern races of corn are the product of teosinte introgression have been examined and found to be unsupported by the available evidence.

1. Hybridization between maize and teosinte is not rare but is common in many localities in Mexico and Guatemala and has presumably been going on for centuries.

2. There is every reason to believe that this hybridization has been accompanied by gene exchange.

3. It has been shown that chromosome knobs can be transferred from teosinte to maize and if knobs are accepted as indicators of teosinte introgression there are abundant cytological manifestations of such introgression.

4. Both circumstantial and direct evidence show that maize can be improved in certain characteristics, including yield, by hybridization with teosinte.

5. No facts have been discovered to support the suggestion that tripsacoid characters in maize are the result of parallel mutations. On the contrary, the fact that several such characters may appear simultaneously points to genetic recombination following hybridization.

New evidence from both prehistoric and living maize support the following additional statements:

6. All recent collections of archaeological maize from caves in Mexico, Arizona, New Mexico, Colorado, Texas and Oklahoma include specimens which can be closely matched by segregates of maize-teosinte hybrids.

7. Archaeological evidence of teosinte introgression is accompanied by increased variability and improvement in certain characteristics.

8. The introgression of teosinte has mutagenic effects, some of which appear to be beneficial.

9. There is some circumstantial evidence of the direct introgression of Tripsacum into maize.

10. Chromosomes having tripsacoid effects have been extracted from corn varieties from Mexico, Honduras,

Nicaragua, Cuba, Venezuela, Brazil, Paraguay, Bolivia and Argentina.

11. The part of the tripartite theory on the origin and evolution of corn which postulates that many modern races are the product of teosinte (or Tripsacum) introgression is now regarded as well established.

LITERATURE CITED

1. Anderson, E. and W. L. Brown, 1952. Origin of Corn Belt maize and its genetic significance. *In* Heterosis: 124–148. Iowa State College Press.

2. Arnason, T. J., 1936. Cytogenetics of hybrids between *Zea mays* and *Euchlaena mexicana*. Genetics 21: 40–60.

3. Beadle, G. W., 1932. Studies of *Euchlaena* and its hybrids with *Zea*. I. Chromosome behavior in *Euchlaena mexicana* and its hybrids with *Zea mays*. Zeitschr. Ind. Abstamm. Vererb. 62: 291–304.

4. ——, 1932. The relation of crossing over to chromosome association in Zea-Euchlaena hybrids. Genetics 17: 481–501.

5. Brown, W. L., 1949. Numbers and distribution of chromosome knobs in United States maize. Genetics 34: 524–536.

6. —— and E. Anderson, 1948. Southern dent corns. Ann. Missouri Bot. Gard. 35: 255–274.

7. Cervantes R., J., A. Rodriguez V. and J. S. Niederhauser, 1958. Resistencia al virus causante del achaparramiento del maíz. Folleto Tecnico 29: 1–18. Secretaria de Agricultura y Ganaderia, Mexico.

8. Collins, G. N., 1921. Teosinte in Mexico. Jour. Hered. 12: 339–350.

9. Cutler, H. C., 1952. A preliminary survey of plant remains of Tularosa Cave. Fieldiana: Anthropology (Chicago Nat. Hist. Mus.) 40: 461–479.

10. —— and E. Anderson, 1941. A preliminary survey of the genus Tripsacum. Ann. Missouri Bot. Gard. 28: 249–269.

11. Emerson, R. A. and G. W. Beadle, 1932. Studies of *Euchlaena* and its hybrids with *Zea*. II. Crossing over between the chromosomes of *Euchlaena* and those of *Zea*. Zeitschr. Ind. Abstamm. Vererb. 62: 305–315.

12. Farquharson, L. I., 1957. Hybridization in Tripsacum and Zea. Jour. Hered. 48: 295–299.

13. Griffing, B. and E. W. Lindstrom, 1954. A study of the combining abilities of corn inbreds having varying proportions of Corn Belt and non-Corn Belt germplasm. Agron. Jour. 46: 545–552.

14. Galinat, W. C., P. C. Mangelsdorf and L. Pierson, 1956. Estimates of teosinte introgression in archaeological maize. Bot. Mus. Leafl. Harvard Univ. 17: 101–124.

15. Graner, E. A. and G. Addison, 1944. Meiose em *Tripsacum australe* Cutler e Anderson (*T. dactyloides* subsp. *hispidum* Hitchcock). Anais da Escola Superior de Agricultura "Luiz de Queiroz." Separata No. 9: 213–224.

16. Harshberger, J. W., 1893. Maize, a botanical and economic study. Contrib. Bot. Lab. Univ. Pennsylvania 1: 75–202.

17. Horowitz, S. and A. H. Marchioni, 1940. Herencia de la resistencia a la langosta en el maiz "amargo." An. Inst. Fito. Santa Catalina 2: 27–52.

18. Kempton, J. H. and W. Popenoe, 1937. Teosinte in Guatemala. Carnegie Inst. Washington Publ. 483: 199–218.

19. Kuwada, Y., 1919. Die Chromosomenzahl von *Zea Mays* L. Jour. Coll. Sci. Imp. Univ. Tokyo, 39: 1–148.

20. Longley, A. E., 1924. Chromosomes in maize and maize relatives. Jour. Agric. Research 28: 673–682.

21. ——, 1937. Morphological characters of teosinte chromosomes. Jour. Agric. Research 54: 835–862.

22. ——, 1938. Chromosomes of maize from North American Indians. Jour. Agric. Research 56: 177–195.

23. ——, 1939. Knob positions on corn chromosomes. Jour. Agric. Research 59: 475–490.

24. ——, 1941. Chromosome morphology in maize and its relatives. Bot. Rev. 7: 263–289.

25. Longley, A. E., 1941. Knob positions on teosinte chromosomes. Jour. Agric. Research 62: 401–413.

26. ——, 1952. Chromosome morphology in maize and its relatives. Bot. Rev. 18: 399–412.

27. Lumholtz, C., 1902. Unknown Mexico. New York, Charles Scribner's Sons.

28. Mangelsdorf, P. C., 1947. The origin and evolution of maize. Advances in Genetics 1: 161–207.

29. ——, 1950. The mystery of corn. Sci. Amer. 183: 20–24.

30. ——, 1952. Hybridization in the evolution of maize. *In* Heterosis: 175–198. Iowa State College Press.

31. ——, 1958. The mutagenic effects of hybridizing maize and teosinte. Cold Spring Harbor. Symp. Quant. Biol. 23: 409–421.

32. —— and J. W. Cameron, 1942. Western Guatemala, a secondary center of origin of cultivated maize varieties. Bot. Mus. Leafl. Harvard Univ. 10: 217–252.

33. —— and R. H. Lister, 1956. Archaeological evidence on the evolution of maize in northwestern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 151–178.

34. ——, R. S. MacNeish and W. C. Galinat, 1956. Archaeological evidence on the diffusion and evolution of maize in northeastern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 125–150.

35. —— and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exp. Sta. Bull. 574: 1–315.

36. —— and R. G. Reeves, 1945. The origin of maize: present status of the problem. Amer. Anthropologist 47: 235–243.

37. —— and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harvard Univ. 13: 213–247.

38. O'Mara, J. G., 1942. A cytogenetic study of Zea and Euchlaena. Missouri Agric. Exp. Sta. Research Bull. 341: 1–16.

39. Paxson, J. B., 1953. Pilosity and hispidulousness of the leaf sheath. Maize Gen. Coöp. News Letter 27: 36–38.

40. Randolph, L. F., 1952. New evidence on the origin of maize. Amer. Nat. 86: 193–202.

41. ——, 1955. History and origin of corn II. Cytogenetic aspects of the origin and evolutionary history of corn. *In* Corn and corn improvement: 16–61. New York, Academic Press.

42. Reeves, R. G., 1944. Chromosome knobs in relation to the origin of maize. Genetics 29: 141–147.

43. ——, 1950. The use of teosinte in the improvement of corn inbreds. Agron. Jour. 42: 248–251.

44. ——, 1953. Comparative morphology of the American Maydeae. Texas Agric. Exp. Sta. Bull. 761: 1–26.

45. Rhoades, M. M., 1955. The cytogenetics of maize. *In* Corn and corn improvement, 123–219. New York, Academic Press.

46. Roberts, L. M., U. J. Grant, R. Ramirez E., W. H. Hatheway and D. L. Smith *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize in Colombia. Nat. Acad. Sci.–Nat. Res. Council. Publ. No. 510: 1–153.

47. Rogers, J. S., 1950. The inheritance of photoperiodic response and tillering in maize-teosinte hybrids. Genetics 35: 513–540.

48. ——, 1950. The inheritance of inflorescence characters in maize-teosinte hybrids. Genetics 35: 541–558.

49. ——, 1950. Fertility relationships in maize-teosinte hybrids. Texas Agric. Exp. Sta. Bull. 730: 1–18.

50. Rosbaco, U. F., 1951. Consideraciones sobre maíces "amargos" con especial referencia a su cultivo en la provincia de Entre Ríos. Idia No. 46: 1–12.

51. Weatherwax, P., 1935. The phylogeny of *Zea Mays*. Amer. Midland Nat. 16: 1–71.

52. ——, 1950. The history of corn. Sci. Month. 71: 50–60.

53. Wellhausen, E. J., L. M. Roberts and E. Hernandez X. *in collaboration with* P. C. Mangelsdorf, 1952. Races of maize in Mexico. Bussey Institution, Harvard Univ. 1–223.

54. —— and C. Prywer, 1954. Relationship between chromosome knob number and yield in corn. Agron. Jour. 46: 507–511.

55. ——, A. Fuentes O. and A. Hernandez C., *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize in Central America. Nat. Acad. Sci.–Nat. Res. Council Publ. 511: 1–128.

56. Vachhani, M. V., 1950. A study of the relationship of chromosome knobs with certain agronomic and morphological characters in corn inbreds. Agron. Jour. 42: 196–201.

57. Venkatraman, T. S. and R. Thomas, 1932. Sugarcane-sorghum hybrids. Indian Jour. Agric. 2: 19–27.

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THE ORIGIN OF CORN

IV. PLACE AND TIME OF ORIGIN

BY

PAUL C. MANGELSDORF AND ROBERT G. REEVES

In regard to the origin of this plant, although there has never been room for reasonable doubt, there have been those who fancied there was room for argument. America is clearly and beyond question the native country of Indian corn. Yet, from the commencement of its history, writers have not been wanting to contest this point, and to claim for it an Eastern origin. The weight of authority and of argument so entirely preponderates in favor of its American origin, that it is scarcely worthwhile, in a work aiming to be useful rather than learned, to waste the time of the reader with idle and unprofitable speculation. —EDWARD ENFIELD (10).

This statement which appeared almost a century ago in an otherwise undistinguished work is as true today as it was then. We supposed when, some twenty years ago, we wrote our monograph on the origin of Indian corn and its relatives (31) that there was one question — its place of origin, America or the Old World — which had been answered once and for all. It turns out that we were wrong; for although our monograph stimulated much useful interest in the problem of the origin of maize, it also opened a veritable Pandora's box of unrestrained speculation on certain aspects of the problem. It has, as a consequence, become necessary once again to review the evidence pertaining to the question of corn's place of origin.

Pre-Columbian Maize in Asia?

Among the herbalists and early botanists who gave their attention to maize, there were a number who regarded it as a plant of Old World origin (cf. 30). The evidence which de Candolle (7) marshalled to support his conclusion on the American origin of maize was so convincing that the problem was then generally regarded as solved. But several times in this century the question of an Asiatic origin or of a pre-Columbian distribution of maize in Asia has been raised. Following the discovery of a previously unknown type of endosperm, "waxy," in a variety of Chinese maize, Collins (9) suggested, despite Laufer's (23) earlier conclusion to the contrary, that maize may have been known in Asia before the discovery of America. More recently Anderson has, on several occasions (1, 2), suggested the possibility of an Asiatic origin of maize or of its prehistoric spread to Asia, and, in a joint paper with Stonor (38) describing some collections of maize from Assam, reached the conclusion that "maize must either have originated in Asia or have been taken there in pre-Columbian times."

The conclusions of Stonor and Anderson were welcomed by the "diffusionists," a school of geographers, anthropologists and others who professed to see in art forms, myths, and other cultural traits, including the use of plants, great similarities between Asia and America and who, for reasons which are not at all clear to us, are apparently determined to prove that all of these traits diffused from a common center. So far as plants are concerned the diffusionists' theses have had the support, especially of Carter (8), Heyerdahl (15), and Sauer (37), all of whom have regarded the conclusions of Anderson or of Stonor and Anderson as supporting the idea of pre-Columbian, trans-Pacific diffusion.

Diffusionists may also have found encouragement in Hatt's (14) fascinating study of American and Indonesian folklore which showed some remarkable similarities between the two, especially with respect to various versions of the Corn Mother myth. For example, the origin of cultivated plants from a sacrificed child, an important motif in Indonesia, is also conspicuous in Peruvian mythology. Nevertheless, Hatt was compelled to conclude that if agriculture and myths reached America across the Pacific Ocean this must have taken place not all at once but at different times, He did not suggest diffusion in the opposite direction nor did he consider it a possibility, as Sauer seems to have, that a Corn Mother myth could have been diffused except as it accompanied the spread of a grain.

The idea of a pre-Columbian interchange of plants between the Old World and the New was virtually demolished by Merrill (33). He showed that there is not only a lack of tangible evidence for such prehistoric diffusion but also that the presence of American plants in Asia soon after the discovery of America is easily and reasonably accounted for by the early Portuguese trade route established in 1500 from Brazil to Goa by way of the Cape of Good Hope.

So far as maize is concerned, the case for its pre-Columbian occurrence in Asia, never a very convincing one, was considerably weakened when Mangelsdorf and Oliver (30) showed that the Assamese maize described by Stonor and Anderson is not at all unique and has close counterparts in Colombia and other parts of South America. The case has recently been weakened still more by new evidence presented by Ho (16) who, after a searching study of Chinese historical sources, concluded that maize was introduced into China early in the sixteenth century arriving there by both overland and maritime routes. He states:

Summing up the introduction of maize into China, we may say that maize was introduced into China two or three decades before 1550; that it was probably introduced by both the overland and maritime routes; that there is little reason to justify Laufer's far-reaching conclusion, especially in the light of the introduction of other New World plants, that in the dissemination of food plants 'a land route is preferred over a sea route as their way of propagation'; and that, barring a sensational discovery in Chinese sources clearly indicating a pre-Columbian introduction, Chinese maize as a topic for anthropological speculation should be closed.

Sutô and Yoshida (39) were doubtless unaware of Ho's paper when they concluded, on the basis of decidedly meager evidence, that one of the types of oriental maize, Persian, described by them must have had an extensive pre-Columbian distribution in parts of Asia. They also favored Anderson's suggestion (2) that corn originated in Asia perhaps as an amphidiploid of a five-chromosome species of *Coix* or *Sorghum*. They were apparently unaware also of the discovery by Barghoorn *et al* (4) of fossil maize pollen in the Valley of Mexico almost identical with that of modern maize pollen. This discovery, to be discussed in more detail later, virtually proves the American origin of corn and rules out the possibility of an Asiatic origin.

Pre-Columbian Corn in Africa?

The confusion which can result from what Enfield has called "idle and unprofitable speculation" is nowhere better illustrated than in Jeffreys' (20) acceptance of that part of the Stonor-Anderson thesis which holds that, if maize did not originate in Asia, it must have been taken there in prehistoric times.

Jeffreys (17) had earlier assembled extensive historical references purporting to show that there had been Arab-Negro contacts with the Americas beginning about 900 A.D. and that maize had been introduced into Africa before 1492. When Goodwin (12) described potsherds

from Ife in Nigeria, apparently decorated by rolling a maize cob over wet clay, Jeffreys (18) proceeded to date the introduction of maize into the region in Africa represented by Ife at 1000–1100 A.D.[1], a date slightly earlier than the one which he had arrived at on the basis of other evidence (19). He then showed by linguistic and historical evidence how it might have spread from Africa to Asia (20).

To analyze Jeffreys' arguments in detail would seem to serve no useful purpose until it should first become clear: (A) that the impressions on the African pottery are unmistakably those of maize[2]; (B) that they are unmistakably pre-Columbian. Unless these two facts can be clearly established, we prefer to agree with Goodwin's recent statement (in a letter) which he has kindly given us permission to quote:

> . . . and am of the opinion that not all of this pottery was decorated by rolling a maize cob over the surface. I have no evidence from that or from any other source suggesting that maize reached Africa in Pre-Columbian times.

Pre-Columbian Maize in Europe?

Finan (11), in a study of the maize illustrated and described in the herbals, concluded that there were two

[1] Weatherwax erroneously attributes to Goodwin the idea of a pre-Columbian introduction of maize into Africa. Goodwin carefully avoided drawing such a conclusion.

[2] We have not been able to obtain specimens of the African potsherds for examination but, since this was written, we have seen photographs of one of them displayed at the Tenth International Congress of Genetics in Montreal by Dr. W. R. Stanton of Nigeria. There is little doubt that this impression is of a maize cob since the paired arrangement of the spikelets is clearly shown. But Stanton, like Goodwin, regards these impressions as post-Columbian and states that he is in general agreement with Porteres (35) who, after carefully reviewing the evidence presented by Jeffreys, Mauny, and others, concluded that maize reached Africa in the sixteenth century by two routes: a flint corn by way of the Mediterranean and the Nile; a soft [probably dent] corn by way of the coast of Guinea.

distinct types: the first, characterized by conspicuous prop roots, was probably a tropical form introduced into Europe from the Caribbean area soon after 1492: the second, which lacks prop roots but sometimes has numerous tillers, is similar to the Northern Flints of eastern North America and appears to have been well known in Europe within 50 years after America's discovery. He (as well as Anderson in the preface to Finan's work) raised the question whether it could have been introduced into Europe by the Norsemen before 1492. Finan also speculated on the reason for the common belief among the herbalists that corn came to Europe from the Orient,

Sutô and Yoshida have gone even further than this in their unqualified assertion that the Aegean type, from which they believed the European maize to be derived and which was first described by Anderson and Brown (3), was, like the Persian, diffused throughout the Old World before 1492.

Corn's Rapid Spread after 1492

If all of these various assertions about pre-Columbian maize in the Old World were true, maize must have been about as widely distributed there as it was in America. Why then did it not leave a single tangible record of any kind of its presence? Why did corn cause such wonderment to sixteenth century students of plants if it had already been known for several centuries or more?

Underlying all of the speculations on pre-Columbian maize in Asia, Africa, or Europe is one common assumption: that corn could not have spread rapidly enough after 1492 to reach all of the places where it was known a generation later. This is not only a highly unreliable premise but also, we think, a presumptuous one for it places arbitrary limits, not justified either by history or

by contemporary experience, on mankind's capacity to spread, through trade and other means, the world's products. So far as Europe and Africa are concerned, the early post-Columbian occurrence of maize is explained quite satisfactorily by Wright (46) who showed how the Moors, after being partially expelled from Spain between 1499 and 1502, took maize with them to Tangier and the north African coast whence it rapidly spread to that part of the world which lay around the Mediterranean Sea, i.e., Turkey, Syria, and Egypt. Wright explains further that the name "Turk" in England during the sixteenth century was often used indiscriminately with "Moor" to indicate a Moslem. It seems probable, therefore, that maize at one period was obtained more easily in western Europe from the Moslem regions of the Mediterranean than from the West Indies and hence was known to the English as "Turkey corn" (both Egypt and Syria were then parts of Turkey) and to the Italians as *grano turco.*

Perhaps the belief, held by a number of the herbalists, that maize came from the East was based on nothing more than the fact that its common name seemed clearly to indicate an eastern origin. Some recent modern conclusions regarding its origin have had little more foundation in fact.

The Place of Origin in America

The discovery by Barghoorn *et al* (4) of fossil pollen in the Valley of Mexico seems now to have established the origin of corn in America beyond question but it still leaves open the problem of where in America maize was first domesticated.

The fossil pollen also proves without doubt that wild maize once grew in the Valley of Mexico. But the fact that maize pollen was found in the drill core only at great depths (below 69 meters) and then was absent until it

appeared again at the upper levels (above 3.6 meters), probably after the establishment of agriculture, suggests that the early fossil maize was that of a colony which became extinguished, perhaps through volcanic action. However, if wild maize grew in one Mexican valley it may well have grown in others and in similar sites in other regions.

Archaeological maize from caves in Mexico and New Mexico—some of it not far removed in its characteristics from wild corn—also points to an early center of domestication in Mexico. Furthermore, the oldest archaeological corn so far discovered in South America—that described by Bird (5) from Huaca Prieta—is later than the earliest corn from either Bat Cave or La Perra Cave and is more advanced in its development. Finally, anthropologists now tend to believe that the prehistoric cultures of America had their beginnings in Middle America and spread from there to South America (45).

For all of these reasons, Mangelsdorf concluded several years ago (26) that "Maize undoubtedly had at least one center of origin in Middle America."

This conclusion is, of course, directly contrary to our earlier one (31) that maize had its origin in the lowlands of South America—an assumption based on the fact that pod corn, which we then regarded and still regard as the ancestral form, was repeatedly encountered there and was apparently unknown in Mexico and Central America. And then, too, with teosinte disposed of as a hybrid of maize and Tripsacum, there no longer seemed to be any compelling reason for looking to the region where teosinte is native as the center of origin of maize. We have never been convinced, as Weatherwax has apparently been (41, 42, 43), that corn's center of origin must coincide with the center of diversity of its relatives, teosinte and Tripsacum.

In spite of the recently discovered evidence for a Middle American origin of cultivated maize—one which has been favored on the basis of other evidence not only by Weatherwax but also by Kempton and Popenoe (21), Kuleshov (22), Meade (32), and Vavilov (40)—we are not yet ready to rule out completely the possibility of an independent center of origin somewhere in South America although our earlier idea of a single origin in the lowlands of South America has now been abandoned.

There are still too many facts which are not completely explained by the assumption of a single origin in Middle America. Among these are: (a) the great diversity of corn in the highlands of Peru; (b) the fact that all of the known pericarp colors of corn occur in one department, Ancash, of Peru (13); (c) the frequent occurrence of pod corn in valleys on the eastern slopes of the Andes; (d) the high incidence of the tu^h gene in Peruvian corn (27); (e) the occurrence in Peru of a primitive race, Confite Morocho, which could conceivably be the progenitor of all of the other known primitive races of the hemisphere (13). So far as the evidence from living corn varieties is concerned, it still points strongly to a South American center in the highlands of Peru, Bolivia and Ecuador and, were it not for the conflicting evidence from fossil pollen and archaeological maize, we should unhesitatingly continue to assume that corn had its origin in South America.

An obvious solution to this dilemma is to assume that maize has been domesticated more than once. Such an assumption would not be radically new. We (31) have previously pointed out that five of the cultivated plants common to Middle America and South America—squashes, beans, tomatoes, amaranths, and cotton—were represented in the two regions by different species or subspecies. There is now evidence that this may have been

true also of corn. There are at least three different primitive races of maize in Peru today (13); two in Colombia (36); and four in Mexico (44). Precursors of two of the Mexican races, Nal-Tel and Chapalote, which in their characteristics are not far removed from wild corn, have been identified in archaeological collections from caves in northeastern Mexico (29) and northwestern Mexico (28). This shows that even in quite early stages of domestication there were already distinct types of corn. One conclusion which might be drawn at this time is that wild corn occurred sporadically in restricted sites in the mountainous region of this hemisphere: in Bolivia, Ecuador, and Peru in South America and in Guatemala and Mexico in Middle America. Once agriculture had been invented and maize domesticated it may have been domesticated repeatedly by the American Indians wherever it was found. Such a conclusion might require modification at any time as the result of the discovery of new archaeological evidence, especially from South America.[3]

In this connection mention should be made of the hypothesis of Birket-Smith (6), based largely on linguistic evidence, that maize originated in Colombia, perhaps in the lower Rio Magdalena Valley. In Colombia there are

[3] Since this was written a study (still unpublished) of the most recent find of archaeological maize from a site in the Ica Valley on the coast of Peru shows that the predominating type of corn is remarkably uniform and is similar, if not identical, to the prehistoric precursor of the still existing Mexican race, Chapalote. Some of the Ica ears, however, show various modifications which can be attributed to introgression from a race of popcorn, Confite Morocho, which is still found in parts of Peru, especially in the Department of Ayacucho. It now appears that the great diversity of maize in Peru had its beginnings when a prehistoric popcorn from Mexico hybridized with the Peruvian popcorn. Whether the Peruvian popcorn was already in cultivation when the Mexican race was introduced cannot be determined from the evidence now available. Additional archaeological evidence from the Peruvian highlands may shed new light on this problem.

names, some of which are regarded as "primitive," associated with maize, its culture and uses, which have affinities with those of Central America, Ecuador, Peru, Venezuela, and the South American lowlands. Roberts *et al* (36) have suggested that such a situation might have developed if this region had been not a center of origin but a crossroads in which the cultures of Central America, the Andean highlands, and the South American lowlands converged. That northern Colombia was definitely a crossroads region is now generally accepted by anthropologists. Evidence from a study of Colombian races of maize tends to support this interpretation. Other aspects of the case for a Colombian origin have been reviewed by Mesa Bernal (34).

The Time of Origin

The fossil maize pollen of Mexico, presumably that of a wild corn, is assigned, on the basis of systematic changes in the frequency of other types of associated pollen, to the last interglacial period. Recent estimates place this at 80,000 years or more ago. There is no reason to doubt that wild maize is much older than this.

The origin of cultivated maize is, of course, much more recent. The oldest archaeological specimens so far studied, those of Bat Cave in New Mexico, are dated by Libby's radiocarbon determinations of associated charcoal at 5,600 years. There is a possibility that the prehistoric maize and charcoal are not contemporaneous; that the charcoal is a residue of fires built by itinerate campers long before the cave was occupied by maize-growing people. This date, however, is not inconsistent with those from other sites. The oldest corn from La Perra Cave, dated by radiocarbon determination of associated vegetal remains at 4445 years, is by no means as primitive as the earliest Bat Cave specimens. The oldest

archaeological maize from Swallow Cave, similar to the earliest Bat Cave material, has not been dated but the fact that it occurred in levels 13 and 14, seven feet below the surface, suggests a very substantial age. The pre-pottery corn from Tm C 247, a site excavated by MacNeish (24, 25), some of which is similar to the Bat Cave corn, has been tentatively dated at 3945 years. The oldest corn from Huaca Prieta in Peru, dated about 2900 years, is already well advanced in its development over the earliest Bat Cave corn.

The evidence, so far as it goes, is consistent with the conclusion that corn was first domesticated about 5000 years ago or perhaps a millennium or more still earlier. How, even in this length of time, could the primitive corn, with which domestication began, have evolved into the highly developed varieties of today such as the Corn-Belt corn of the United States with its magnificent ears or the spectacular large-seeded flour corn of the region of Cuzco, Peru? This is a question to which we hope that the earlier papers in this series will have given, at least, some of the answers.

LITERATURE CITED

1. Anderson, E., 1943. A variety of maize from the Rio Loa. Ann. Missouri Bot. Gard. 30: 469–474.

2. ——, 1945. What is *Zea Mays?* Chronica Botanica 9: 88–92.

3. —— and W. L. Brown, 1953. The popcorns of Turkey. Ann. Missouri Bot. Gard. 40: 33–48.

4. Barghoorn, E. S., M. K. Wolfe and K. H. Clisby, 1954. Fossil maize from the Valley of Mexico. Bot. Mus. Leafl. Harvard Univ. 16: 229–240.

5. Bird, J., 1948. America's oldest farmers. Nat. Hist. 57: 296–303, 334–335.

6. Birket-Smith, K., 1943. The origin of maize cultivation. Kgl. Danske Videnskabernes Selskab; Hist.—Filol. Meddel 29: 1–49.

7. Candolle, A. de, 1886. Origin of cultivated plants. Reprint of 2nd edition, 1959. New York, Hafner Publishing Co.

8. Carter, G. F., 1950. Plant evidence for early contacts with America. Southwest Jour. Anthrop. 6: 161–182.

9. Collins, G. N., 1909. A new type of Indian corn from China. U. S. Dept. Agric. Bur. Plant Industry Bull. 161: 1–30.

10. Enfield, E., 1866. Indian corn, its value, culture and uses. New York, D. Appleton and Co.

11. Finan, J. J., 1950. Maize in the great herbals. Waltham, Mass., Chronica Botanica.

12. Goodwin, A. J. H., 1953. The origin of maize. S. African Arch. Bull. 29: 13–14.

13. Grobman, A., W. Salhuana and P. C. Mangelsdorf, 1956. Races of maize in Peru. Maize Gen. Coöp. News Letter 30: 27–30.

14. Hatt, G., 1951. The Corn Mother in America and in Indonesia. Anthropos 46: 853–914.

15. Heyerdahl, T., 1952. American Indians in the Pacific; the theory behind the Kon-Tiki expedition. London, George Allen & Unwin Ltd.

16. Ho, P. T., 1956. The introduction of American food plants into China. Amer. Anthrop. 57: 191–201.

17. Jeffreys, M. D. W., 1953. Pre-Columbian negroes in America. Scientia (July–Aug.), 1–18.

18. ——, 1953. Pre-Columbian maize in Africa. Nature 172: 965–966.

19. ——, 1953. The history of maize in Africa. Eastern Anthrop. 7: 138–147.

20. ——, 1955. Pre-Columbian maize in Asia. Eastern Anthrop. 9: 21–28.

21. Kempton, J. H. and W. Popenoe, 1937. Teosinte in Guatemala. Carnegie Inst. Washington Publ. 483: 199–218.

22. Kuleshov, N. N., 1929. Geographical distribution of the diverse varieties of maize in the world. Bull. Appl. Bot. Gen. Pl. Breeding 20: 506–510.

23. Laufer, B., 1907. The introduction of maize into Eastern Asia. Proc. 15th Intern. Congr. Americanists 1: 223–257.

24. MacNeish, R. S., 1955. Ancient maize and Mexico. Archaeology 8: 108–115.

25. ——, 1958. Preliminary archaeological investigations in the Sierra de Tamaulipas, Mexico. Trans. Amer. Philos. Soc. 48, pt. 6: 1–210.

26. Mangelsdorf, P. C., 1954. New evidence on the origin and ancestry of maize. Amer. Antiquity 19: 409–410.

27. ——, 1957. Half-tunicate from Peru, Ecuador and Paraguay. Maize Gen. Coöp. News Letter 31: 64.

28. —— and R. H. Lister, 1956. Archaeological evidence on the evolution of maize in northwestern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 151–178.

29. ——, R. S. MacNeish and W. C. Galinat, 1956. Archaeological evidence on the diffusion and evolution of maize in northeastern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 125–150.

30. —— and D. L. Oliver, 1951. Whence came maize to Asia? Bot. Mus. Leafl. Harvard Univ. 14: 263–291.

31. Mangelsdorf, P. C. and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exp. Sta. Bull. 574.

32. Meade, J., 1948. Iziz Centli (El Maíz). Mexico.

33. Merrill, E. D., 1954. The botany of Cook's voyages. Waltham, Mass., Chronica Botanica.

34. Mesa Bernal, D., 1957. Historia natural del maiz. Revista Acad. Colomb. Cien. Exact. Fis. Nat. 10: 13–106.

35. Porteres, R., 1955. L'introduction du mais en Afrique. Jour. Agric. Trop. Bot. Appl. 2: 221–231.

36. Roberts, L. M., U. J. Grant, R. Ramirez E., W. H. Hatheway and D. L. Smith, *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize in Colombia. Nat. Acad. Sci.-Nat. Res. Council Publ. No. 510.

37. Sauer, C. O., 1952. Agricultural origins and dispersals. New York, Amer. Geog. Soc.

38. Stonor, C. R. and E. Anderson. 1949. Maize among the hill peoples of Assam. Ann. Missouri Bot. Gard. 36: 355–404.

39. Sutô, T. and Y. Yoshida, 1956. Characteristics of the Oriental maize. *In* Land and Crops of Nepal Himalaya II: 373–529.

40. Vavilov, N. I., 1931. Mexico and Central America as the principal center of origin of cultivated plants of the New World. Bull. Appl. Bot. Gen. Pl. Breeding 26: 179–199.

41. Weatherwax, P., 1923. The story of the maize plant. Univ. Chicago Press.

42. ——, 1936. The origin of the maize plant and maize agriculture in ancient America. Univ. New Mexico Bull. (October), 1–8.

43. ——, 1954. Indian corn in old America. New York, Macmillan.

44. Wellhausen, E. J., A. Fuentes O. and A. Hernandez C., *in collaboration with* P. C. Mangelsdorf, 1957. Races of maize in Central America. Nat. Acad. Sci.-Nat. Res. Council Publ. No. 511.

45. Willey, G. R., 1955. The prehistoric civilizations of nuclear America. Amer. Anthrop. 57: 571–593.

46. Wright, A. C. A., 1949. Maize names as indicators of economic contacts. Uganda Jour. 13: 61–81.

THE ORIGIN OF CORN

V. A Critique of Current Theories

BY

ROBERT G. REEVES AND PAUL C. MANGELSDORF

IN the previous papers in this series (22, 23, 24, 32), we have reviewed the objections to and the evidence supporting our tripartite theory on the origin and evolution of corn. We have shown that the factual evidence for some parts of this theory has increased substantially during the last two decades, and that nothing has yet come to our attention which completely rules out any part of it.

The hypothesis that the original corn was a type of pod corn is all but proven by archaeological evidence and by a genetic reconstruction of the ancestral form (15, 16, 17, 19, 20). Because of the discovery of fossil corn pollen in Mexico, the view that corn originated in South America is less satisfactory now than it was twenty years ago, but the hypothesis of a South American origin is not yet completely untenable since research on some phases of this problem, such as that on fossil pollen, has only begun.

The evidence that teosinte (*Zea mexicana*) originated as a hybrid between corn and Tripsacum is decidedly stronger now than when the hypothesis was first presented and, contrary to opinions of several other workers, there is no sound evidence against the hypothesis. We have always recognized that this part of the tripartite theory cannot easily be tested. We have never consid-

ered the probability to be great that a "good" teosinte could be synthesized by hybridizing corn and Tripsacum in experimental cultures, and we have given reasons for this.

The recent evidence is decidedly in favor of the view that introgression between corn and teosinte has been frequent and that it has been effective in producing innumerable new varieties and forms, both ancient and modern. We now consider that this third part of the tripartite theory is almost an established fact.

It should be clear from the contents of previous papers in this series that we consider the tripartite theory to be better supported by factual evidence than any other explanation of the origin of corn proposed up to the present. The fact that we are still committed to the tripartite theory, however, should not prevent us from considering alternative theories and this we shall attempt to do objectively, if briefly, in this final paper.

The Papyrescent (*Semivestidos*) Theory

This is no more than a slight modification of the pod-corn theory. Andres (1) discovered in Argentine maize a type which superficially resembles a weak form of pod corn. Apparently unaware that Bonvicini (5) in Italy had described this character many years earlier and had given it the name "palee sviluppate," Andres called the type "semivestidos" and suggested that it, rather than pod corn, might be the ancestral form.

The character has recently been given still a third and probably more appropriate name "papyrescent" by Galinat (10), whose studies show that the glumes of this type become soft and papery as they mature. Unlike pod corn, which although sometimes monstrous still represents a combination of normal characteristics found in other grasses, papyrescent is a defect in development which it

is difficult to regard as constituting the primitive form of modern corn. No archaeological specimens of papyrescent corn have been reported.

As was pointed out in the first paper in this series, Weatherwax (41), in discussing one aspect of the pod-corn theory, apparently confused papyrescent maize and a weak form of pod corn, half-tunicate. His illustration (Fig. 51) of half-tunicate maize is almost certainly a photograph of papyrescent maize.

The Corn Grass Theory

Singleton (35) has suggested that the ancestral form of modern corn is "corn grass." This anomalous type, the product of a single dominant gene, produces numerous tillers and small "ears" with a high proportion of single spikelets. Many of the kernels are partly enclosed in bracts, but the majority of these are not glumes but spathes.

He also suggested that, if a plant of corn grass were found in nature, it would not be recognized as maize and would almost certainly be regarded as a different species if not a different genus. This may be true, and it illustrates how the maize plant can be drastically changed by a single gene mutation. If corn grass were the ancestral form, a mutation at a single locus could have transformed it from a wild, almost useless, plant to the unique cereal which maize is today.

Although corn grass has some of the characteristics which we might expect to find in an ancestral form — for example, a freely-tillering habit — it lacks others, such as the regular development of prominent glumes. At the other extreme, it has characters which are not demanded of a hypothetical ancestor. One of these, single spikelets (9), represents a condition more specialized instead of more primitive than the paired spikelets of mod-

ern maize. Another, a well-developed spathe, suggests the ancestral form not of maize but of *Coix*, whose fruit case has been found by Weatherwax (39) to comprise a spathe and a segment of the rachis. Corn grass probably is, as Galinat (8) has suggested, a "false" progenitor of maize, exhibiting certain traits which might have occurred in a remote ancestor of the *Maydeae*.

Finally, the evidence from archaeological maize does not support the corn grass theory. Prehistoric maize had prominent glumes, but it did not have the long spathes of corn grass. The possibility that corn grass is the ancestral form appears to us to be remote indeed.

The Teosinte Theory

The theory that maize originated as a domesticated form of teosinte—its nearest known relative—was first proposed by Ascherson (2). Later students, notably Harshberger (12) and Collins (6), modified the theory postulating that one parent of corn is teosinte and the other is a grass now unknown. As teosinte occurs naturally only in Mexico and Central America, supporters of this theory have usually assumed that both teosinte and maize originated in that region. We (21) concluded that teosinte is the progeny rather than the progenitor of maize — the product of the natural hybridization of maize and its wild relative, Tripsacum. Teosinte, however, plays an important role in the tripartite theory, for this theory holds that the many modern varieties of maize are the product of the introgression of teosinte into maize.

Since 1939, new evidence has been presented both in support of and in contradiction to the teosinte theory.

Beadle's (4) discovery that the seeds of teosinte will "pop" when exposed to heat, shattering the hard, bony shell in which they are enclosed, shows one way in which teosinte might have been used as a food plant and weak-

ens the objection that a species so unpromising for food purposes would never have been domesticated. There is no evidence, however, archaeological, historical or contemporary, to show that teosinte was ever employed for food in this manner. When teosinte is used for food, as it occasionally is today in times of food shortage, the fruits are crushed on a metate or with a mortar and pestle, and the meal of the crushed caryopses is separated from the fragments of the bony fruit case.[1]

Langham's (13) data on the inheritance of characteristics which distinguish teosinte and maize indicate simple Mendelian inheritance for several characters and lend some support to Emerson's (unpublished) contention that a few large scale mutations could transform teosinte into maize. But the much more extensive data of Mangelsdorf (14) and of Rogers (33, 34) show that the genes which distinguish maize and teosinte are numerous and are distributed among a majority of the chromosomes. The highly significant studies of Rogers seem to have been completley overlooked by both Weatherwax and Randolph; at least they are not cited in their extensive bibliographies.

The recent studies of Barghoorn, Wolfe and Clisby (3) on fossil pollen in Mexico lend no support to the teosinte theory. Although pollen of both maize and Tripsacum was found at great depths, the pollen of teosinte occurred only near the surface in the upper levels of the drill core where maize pollen was abundant suggesting that the practice of agriculture had begun. Furthermore, the maize pollen found at the lower levels is as large as any modern maize pollen and shows no resemblance to teosinte pollen in the ratio of total diameter to the diameter of its pore. If this fossil pollen is as old as it is estimated to be — 80,000 years or more — the

[1] Personal communication from the late R. H. Barlow.

theory that maize originated from teosinte under domestication can now be safely ruled out.

Recent studies of archaeological maize, like those of fossil pollen, do not support the teosinte theory. On the contrary, they show that the earliest maize was less like teosinte, whereas some recent maize is more like it. Archaeological specimens exhibiting characteristics of teosinte, including distichous ears, single spikelets and highly lignified rachises and glumes, have been found in several sites. But these are always recent specimens and are interpreted as being products of the introgression of teosinte into cultivated maize (7, 11, 19, 20, 25).

A series of studies on the morphology of the corn ear has a bearing on the teosinte theory, because many workers who favored this theory explained the polystichous character of the corn ear as the result of the lateral fusion of several teosinte spikes. The voluminous literature on this subject was reviewed by Mangelsdorf and Reeves in 1939 (21) and more recently by Nickerson (27). The present status of the problem is that evidence for the lateral fusion of two-rowed spikes to form the polystichous ear is completely lacking; the only evidence found for fusion is the adnation of the rachis flaps (prophylls) to the main axis of the cob. It may be concluded, therefore, that the structure of the corn ear has thus far shown no evidence that corn is a descendant of teosinte.

The Theory of Common Ancestry

It appears that Montgomery (26) was the first to propose the theory of common ancestry, although he did not include Tripsacum in the alliance with corn and teosinte. Weatherwax (37) formulated the theory as we now know it, by adding Tripsacum to the two species considered by Montgomery, and he defended it in subsequent publications (38, 40, 41, 42). Randolph (28, 29)

agreed with Weatherwax, with reservations; he still regards the direct descent of corn from teosinte as a distinct possibility.

The theory of common ancestry maintains that corn originated from a perennial, wild, corn-like ancestor, now extinct, and that this extinct ancestor, sometimes called pre-maize, in turn had an ancestor, likewise extinct, in common with teosinte and Tripsacum; also that the native range of all of these species was Central America and Mexico. Actually the theory represents the application to the American *Maydeae* of the broad views of Darwin and earlier students of evolution.

The factual evidence claimed by the proponents of this theory falls into two categories. (A) The three groups—corn, teosinte and Tripsacum—are very similar, except that each has modifications of its own which have led to the differences now found among them. For example, teosinte and Tripsacum have lost one member of each original pair of pistillate spikelets, but corn has not; most varieties of corn and teosinte have lost the terminal staminate portion of the lateral inflorescence (ear), but Tripsacum has not. Weatherwax (41, 42) pointed out by way of explanation that, if we could restore to each of the three groups the primitive organs which have been modified in evolution, they would converge in a common type, giving us an idea of the common ancestor. But more revealing, in our opinion, is the result that would be obtained by restoring the primitive organs of only corn and Tripsacum, omitting teosinte. The common type towards which they would converge is the same as when teosinte is included. This fact is best explained by the hypothesis of the hybrid origin of teosinte, because this hypothesis holds that the characters of teosinte are merely a combination of those of corn and Tripsacum.

(B) It is stated that corn, teosinte and Tripsacum are

now sympatric only in Central America and Mexico, and for this reason all of them probably originated from a common ancestor which also occurred there. When the fallacy of placing such strong reliance on this present-day distribution is recognized, little or no factual evidence for the theory of common ancestry remains. Stebbins (36) reviews the literature on the theory that centers of diversity correspond to centers of origin. He points out that the theory has many pitfalls, except when the group in question is young and the selective forces of the environment have been operating in about the same manner throughout its evolutionary history. Stebbins shows that related genera, congeneric species and even conspecific populations might be expected to have widely disjunct ranges. He cites numerous examples of a single species with two ranges separated by half the distance around the earth. He shows also that examples of closely related disjunct taxa are not rare exceptions but are numerous and that some of them have been known since the time of Darwin.

Much of the validity of the Montgomery-Weatherwax theory depends upon the assumed correlation between the common ancestry and the common place of origin of the three groups. If one or two of the groups were shown to have originated elsewhere than in the present center of diversity (and this may yet prove to be true especially of Tripsacum), this would seriously weaken the theory. In addition, the proponents of the theory assume the previous existence of a pre-maize and of the common ancestor of pre-maize, teosinte and Tripsacum without one iota of evidence. The tripartite theory, in contrast, is more flexible and much less dependent upon completely unknown ancestors of corn. Indeed, it requires no ancestral types other than forms still in existence. Types of pod corn very similar to our hypothetical an-

cestor occur today; types of Tripsacum and corn which come extremely near to satisfying the requirements for the putative parents of teosinte are well known. Yet Weatherwax (41, 42) states that it is the tripartite theory, rather than the "simple" theory of common ancestry, which "is topheavy with assumptions of such character that if one of them should be rejected the whole structure would fall."

The theory of common ancestry has two additional weaknesses which are serious: (A) It does not, Weatherwax's and Randolph's contentions to the contrary, notwithstanding, explain all of the known facts. (B) It can not easily be tested.

A. Some of the facts which the theory of common ancestry does not explain are discussed in detail in other papers of this series (23, 32). Here it will suffice to point out that the theory does not account for the facts that (a) teosinte is intermediate between maize and Tripsacum in a great majority of its characteristics (21, 31); (b) early archaeological maize is more "maize-like" than later maize (7, 11, 19, 20, 25); (c) fossil pollen of maize and Tripsacum were found at great depths at one site in Mexico, whereas teosinte pollen occurred only in the upper levels of the drill core; (d) forms of pod corn are now in existence which possess all of the characteristics expected in the ancestral form (16, 17); (e) variation in knob numbers is correlated with tripsacoid characteristics (18), and with proximity to Guatemala, the reputed center of origin of teosinte (21, 30).

B. The theory is largely untestable, because the only evidence which could prove it to be correct beyond a reasonable doubt would be the discovery of prehistoric remains, antedating agriculture, of all three groups of the American *Maydeae* and of the remote ancestor from which these three groups stem. Since it is largely untest-

able, it neither stimulates new research nor points to possible new methods of maize improvement. In this respect, the theory is less useful than the tripartite theory which has furnished the impetus for an extensive series of researches on maize and its relatives and has also suggested new possibilities for improving maize. If two theories appear to be equal in validity, the one which is testable and which stimulates new research is the more useful; a theory which is plausible but untestable tends to stifle research.

In emphasizing the differences between the tripartite theory and that of common ancestry it should not be overlooked that there are also important resemblances between them. The two theories agree that (a) corn is an American plant; (b) it is descended, with Tripsacum, from a remote common ancestor; (c) its immediate ancestor was a freely-branching plant bearing small ears with grains enclosed in glumes; (d) corn attained its present form through changes occurring during domestication, which began not more than a few thousand years ago. In a broad sense, then, the two theories agree with respect to the place, time and manner of origin. In the same broad sense, the problem of the origin of corn can almost be said to be solved.

LITERATURE CITED

1. Andres, J. M., 1950. Granos semivestidos, restos de un carácter ancestral del maiz. Revista Argentina de Agron. 17: 252–256.

2. Ascherson, P., 1875. Ueber *Euchlaena mexicana* Schrad. Bot. Vereins Prov. Brandenburg 17: 76–80.

3. Barghoorn, E. S., M. K. Wolfe and K. H. Clisby, 1954. Fossil remains from the Valley of Mexico. Bot. Mus. Leafl. Harvard Univ. 16: 229–240.

4. Beadle, G. W., 1939. Teosinte and the origin of maize. Jour. Hered. 30: 245–247.

5. Bonvicini, M., 1932. Sulla eraditarietà di una anomalia nel mais. L'Italia Agricola 69: 3–9.

6. Collins, G. N., 1912. Origin of maize. Jour. Washington Acad. Sci. 2: 520–530.

7. Cutler, H. C., 1952. A preliminary survey of plant remains of Tularosa Cave. Fieldiana: Anthropology (Chicago Nat. Hist. Mus.) 40: 461–479.

8. Galinat, W. C., 1954. Corn grass I. Corn grass as a possible prototype or a false progenitor of maize. Amer. Nat. 88: 101–104.

9. ——, 1954. Corn grass II. Effect of the corn grass gene on the development of the maize inflorescence. Amer. Jour. Bot. 41: 803–806.

10. ——, 1957. The effects of certain genes on the outer pistillate glume of maize. Bot. Mus. Leafl. Harvard Univ. 18: 57–76.

11. ——, P. C. Mangelsdorf and L. Pierson, 1956. Estimates of teosinte introgression in archaeological maize. Bot. Mus. Leafl. Harvard Univ. 17: 101–124.

12. Harshberger, J. W., 1896. Fertile crosses of teosinte and maize. Gard. and Forest 9: 522–523.

13. Langham, D. G., 1940. The inheritance of intergeneric differences in Zea-Euchlaena hybrids. Genetics 25: 88–107.

14. Mangelsdorf, P. C., 1947. The origin and evolution of maize. Advances in Genetics 1: 161–207.

15. ——, 1948. The role of pod corn in the origin and evolution of maize. Ann. Missouri Bot. Gard. 35: 377–406.

16. ——, 1958. Reconstructing the ancestor of corn. Proc. Amer. Philos. Soc. 102: 454–463.

17. ——, 1958. Ancestor of corn. Science 128: 1313–1320.

18. —— and J. W. Cameron, 1942. Western Guatemala, a secondary center of origin of cultivated maize varieties. Bot. Mus. Leafl. Harvard Univ. 10: 217–252.

19. —— and R. H. Lister, 1956. Archaeological evidence on the evolution of maize in northwestern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 151–178.

20. ——, R. S. MacNeish and W. C. Galinat, 1956. Archaeological evidence on the diffusion and evolution of maize in northeastern Mexico. Bot. Mus. Leafl. Harvard Univ. 17: 125–150.

21. —— and R. G. Reeves, 1939. The origin of Indian corn and its relatives. Texas Agric. Exp. Sta. Bull. 574: 1–315.

22. —— and R. G. Reeves, 1959. The origin of corn. I. Pod corn, the ancestral form. Bot. Mus. Leafl. Harvard Univ. 18: 329–356.

23. —— and R. G. Reeves, 1959. The origin of corn. III. Modern races, the product of teosinte introgression. Bot. Mus. Leafl. Harvard Univ. 18: 389–411.

24. —— and R. G. Reeves, 1959. The origin of corn. IV. Place and time of origin. Bot. Mus. Leafl. Harvard Univ. 18: 413–427.

25. —— and C. E. Smith, Jr., 1949. New archaeological evidence on evolution in maize. Bot. Mus. Leafl. Harvard Univ. 13: 213–247.

26. Montgomery, E. G., 1906. What is an ear of corn? Pop. Sci. Month. 68: 55–62.

27. Nickerson, N. H., 1954. Morphological analysis of the maize ear. Amer. Jour. Bot. 41: 87–92.

28. Randolph, L. F., 1952. New evidence on the origin of maize. Amer. Nat. 86: 193–202.

29. Randolph, L. F., 1955. History and origin of corn II. Cytogenetic aspects of the origin and evolutionary history of corn. *In* Corn and corn improvement: 16–61. New York, Academic Press.

30. Reeves, R. G., 1944. Chromosome knobs in relation to the origin of maize. Genetics 29: 141–147.

31. ——, 1953. Comparative morphology of the American Maydeae. Texas Agric. Exp. Sta. Bull. 761: 1–26.

32. —— and P. C. Mangelsdorf, 1959. The origin of corn. II. Teosinte, a hybrid of corn and Tripsacum. Bot. Mus. Leafl. Harvard Univ. 18: 357–387.

33. Rogers, J. S., 1950. The inheritance of photoperiodic response and tillering in maize-teosinte hybrids. Genetics 35: 513–540.

34. ——, 1950. The inheritance of inflorescence characters in maize-teosinte hybrids. Genetics 35: 541–558.

35. Singleton, W. R., 1951. Inheritance of corn grass, a macromutation in maize, and its possible significance as an ancestral type. Amer. Nat. 85: 81–86.

36. Stebbins, G. L., Jr., 1950. Variation and evolution in plants. New York, Columbia Univ. Press.

37. Weatherwax, P., 1918. The evolution of maize. Bull. Torrey Bot. Club 45: 309–342.

38. ——, 1919. The ancestry of maize — a reply to criticism. Bull. Torrey Bot. Club 46: 275–278.

39. ——, 1926. Comparative morphology of the oriental Maydeae. Indiana Univ. Studies 73: 3–18.

40. ——, 1950. The history of corn. Sci. Month. 71: 50–60.

41. ——, 1954. Indian corn in old America. New York, Macmillan.

42. ——, 1955. History and origin of corn I. Early history of corn and theories as to its origin. *In* Corn and corn improvement: 1–16. New York, Academic Press.